On the periodicity of tree-growth in the tropics, with reference to the mode of branching, the leaf-fall, and the formation of the resting bud.

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(with 3 text-figures)

CONTENTS

	Page
§ 1. Introduction	13
§ 2. The climate of Singapore	13
§ 3. Periodicity of tree-growth in its relation to the mode of branching	15
§ 4. Materials and methods	16
§ 5. Terminal growth	17
§ 6. Lateral growth	18
1. Substituting growth	19
2. Apposing growth	19
§ 7. Evergrowing trees	20
1. The terminal evergrowing	20
2. The evergrowing tree with lateral growth	23
§ 8. Trees with branches of manifold growth	24
1. Terminal manifold growth	25
2. Lateral manifold growth	26
§ 9. Intermittent growth	27
§ 10. The transition from evergrowing to intermittent	28
§ 11. Deciduous trees	30
1. Transition from intermittent-evergreen to deciduous	30
2. The leaf-period and the date of leaf-fall and leafing	31
§ 12. The flowering season	32
1. The flowering of evergrowing trees	33
2. Seasonal flowering	33
3. Contemporary flowering	34
4. Non-seasonal flowering	35

Page

§ 13. The fruiting season 36

§ 14. The frequency of species of the four types of periodicity . 37

§ 15. Comparison of the leaf-fall and leafing periods of Singapore with those of Ceylon and Java . . . 38

§ 16. The grade of leaf-fall of trees in various districts . . 42

§ 17. The deciduous habit and the height of crown . . 43

§ 18. Deciduous trees and their habitats 44

§ 19. The systematic occurrence of deciduous trees . . 46

§ 20. The geographical distribution of deciduous trees . . 47

§ 21. The geological change of the Malay Peninsula in the past 49

§ 22. The transition of shoot-growth from evergrowing to deciduous (Fig. 1) 51

§ 23. The morphological development of the resting bud with special reference to the formation of scales. The axillary buds (Fig. 2) 54

§ 24. The retrogression of the bud-forming ability . . 57

§ 25. The intermediation of hormonal activity on the process of periodicity (Fig. 3) 58

§ 26. Conclusion 62

§ 27. Summary 63

Appendix 66

Literature cited 80

§ 1. Introduction

During my stay at Singapore, from 1942 to 1945, it was quite unexpected to find that there were such various growth-forms of trees compared with the temperate region. In temperate countries deciduous trees are clearly distinguishable from the evergreen, and leaf-fall is in accordance with the winter. Even a slight fluctuation of chilly weather affects the date of leaf-fall, so that the exacting influence of the climate is conspicuous. This holds true, also, in the monsoon region with a dry season.

In Singapore, most trees are naturally evergreen, and some of them are evergrowing in accordance with the favourable climate, but most of the evergreens are intermittent in their growth and some are even deciduous in spite of so uniform a climate, though the bare spell is very short and the flowering or fruiting may go on during that time. Besides, there are some trees, in which the leafing, flowering, etc. are different according to individual branches or stocks. So we can see among trees every possible transition of growth-form from the evergrowing to the deciduous.

Another peculiarity to be pointed out in Singapore is that the leaf-fall does not coincide with the calendar year. Beside those which shed leaves once, twice, or thrice seasonally every year, there are those which shed leaves from every several months to more than one year non-seasonally. Yet there is no exacting change of climate to enforce this leaf-fall, since other trees or even other stocks of the same species remain clad with a green crown.

To elucidate why such diverse behaviour of the tree-growth is displayed was the chief aim of the present investigation.

The periodicity of tree-growth is a natural consequence of the activity of the growing point. But before discussing the detail, it is necessary first to consider the climatic character of the region. As to general features, one may refer to manuals of climatology and related literature.

§ 2. The climate of Singapore

As is well known, south-eastern Asia and Malaysia undergo, as monsoon regions, a distinct dry season alternatively. But in Singapore, lying just between those two regions, the monsoon effect is extremely moderated and there is no truly dry season. The climate is warm and wet, often cloudy, with insolation neither very long nor intense.

The most definite seasonal feature is the rainy season from October to January. The monthly rainfall amounts to 20 cm. occasionally more than 30 cm. (HOLTTUM '40). The excess of precipitation, however, does not affect the tree-growth particularly, as it is drained away by the surface run-off and seepage, though it is beneficial to the seasonal growth of fungi (CORNER '35).

On the other hand a long spell of rainless days, together with intense radiation, affects the periodicity of trees not a little. The seasonal colour of tree-growth may be attributed mainly to such occurrences. The so-called dry spells occur in Singapore twice a year, February to March and July to August, and correspond nearly to the dry season of India and Malaysia respectively. On the mainland of the Malay Peninsula, however, the distribution of the dry season is not the same; it is different on each side of the coast, as well as inland (STEWART '30).

In Singapore, even in the dry months, the rain-fall amounts usually to 13–16 cm., rarely 6 cm. According to HOLTTUM ('40) the number of times in which the monthly rainfall was less than 2·5 inches (= 6·3 cm.) during 50 years (1890–1939) was twenty-two, or once every two years (see Tab. 1a), and the longest drought during 10 years (1927–1937) was 22 days extending from January to February. The frequency of rainless days, continued for 14–20 (Tab. 1b) and 7–13 days (Tab. 1c) respectively during that time, was as follows:—

TABLE I.—DISTRIBUTION OF THE RAINLESS MONTHS IN SINGAPORE

Month	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	XII	
a	..	..	7	3	1	..	..	6	3	2	..	..	..	during 50 years
b	..	..	1	..	..	..	..	4	..	..	..	1	during 10 years
c	..	2	4	5	1	5	3	9	2	4	2	..	1	during 10 years

From these data it is discernible that the rainless month can shift one month or more according to the year, indicating the non-seasonal character of drought in Singapore.

As long as the dry spell continues, the temperature rises day by day, and the decrease of humidity is more acute. Intense radiation and decrease of water-content by transpiration seem to induce anthogenesis and accelerate leaf-fall as well. A shower after the dry spell causes, then, new leafing often conspicuously. At any rate, as the climate is fairly uniform, even a short dry spell can give rise to the periodic feature of tree-growth.

Naturally the trees which respond in this way are not very abundant, or are restricted to their susceptible phase only, while others show no special reaction to such a triflng change of climate. Even

among deciduous trees there are those which maintain their proper periodicity regardless of the dry spell.

If one compares the periodicity of tree-growth in Singapore with that of the monsoon regions, north and south, or of the tropics of other continents, one finds that there are some kinds of trees that are evergreen in Singapore, while deciduous in other regions. In this respect, Singapore is one of the most uniform climates in the tropics, and moreover with abundance of tree-species. But, then, why in the district of such a uniform climate such various growth-forms occur, is a question to be considered further.

§ 3. The periodicity of tree-growth in its relation to the mode of branching

The periodicity of tree-growth is derived from the behaviour of the growing point. If all twigs grow continually, producing leaves successively, the tree is "evergrowing". If however the growing point ceases to grow or slows down after forming a certain number of leaves, or tends to form an inflorescence, the growth of the twig becomes intermittent.

But, even if some twigs cease to grow or become flowering twigs, the tree is still evergrowing as a whole, provided that some axillary buds are growing into new twigs. The periodicity is, therefore, not only related with the activity of the single shoot-apex, but also with the mode of branching of trees. Such individual differences in branch-growth in the tropics was noted by SCHIMPER ('98) and various subsequent authors. We may designate it the *manifold growth* of tree-branches.

This behaviour is seen not merely in individual branches or limbs of one tree, but also among trees of the same species. That is, some stocks are just in new leaf, while others are clad with dark green old leaves or in flower—the "stockwise manifold growth", in contrast to the "branchwise manifold growth" on the same tree. Among young avenue trees of *Spathodea campanulata* both forms of manifold growth can be seen, while in old trees all stages of the branchwise manifoldness are mingled together in each tree, so that the stockwise difference ultimately disappears.

Now, trees with intermittent growth are very common in the tropics. New leaf-sprays all over the twigs are often seen. If leaves of the previous season still remain at that time, the tree is evergreen just as in the temperate zone, but if they have fallen off beforehand, it is deciduous, though in the tropics there are various transitions.

The periodicity of the tree-growth is determined therefore in two ways:—

(1) whether the activity of growing points is continuous, manifold or intermittent, and

(2) how the growing points are distributed in each branch, terminal or lateral.

The mode of branching in general is well known morphologically, but the periodicity of tree-growth is characterized also by the behaviour of the growing point, which is rather diverse and not always intermittent in the tropics and qualifies the periodical character.

By the combination of these two processes, we get six types of tree-growths as mentioned below:—

THE MODE OF GROWTH AND BRANCHING, AND THEIR COMBINATIONS

(1) Activity of growing point { evergrowing / manifold / intermittent } evergreen or deciduous

(2) Site of growing points in the twig { terminal / lateral }

(3) Mode of growth of tree { terminal-evergrowing / lateral-evergrowing / terminal-manifold / lateral-manifold / terminal-intermittent / lateral-intermittent } { evergreen / deciduous }

§ 4. Materials and methods

Trees examined were those:—

(1) Planted in the Botanic Gardens of Singapore, including exotic trees,

(2) of the *primary* forest of the Gardens,

(3) of Bukit Timah Forest Reserve,

(4) of the *primary* forests of the Water Catchment Area,

(5) of various other places on the Island and the Peninsula.

The identification of wild trees was entirely dependent on the instruction of Mr. E. J. H. Corner, without whose help the present research could hardly have been accomplished. Dr. R. E. Holttum gave me also advice concerning the leaf-fall. I express here my sincerest thanks to them on this occasion.

To classify the growth-types of trees, as mentioned above, is however not always easy. Especially the distinction of the evergrowing from the intermittent is difficult, as there is no sharp distinction between them (§ 10). If one can see the fresh foliage all

over the twigs, as often is the case in jungles, avenues and gardens, it is certain that the tree is intermittent in its growth, but if one can not catch such a chance, it is necessary to investigate the following accessory criteria:—

(1) In evergrowing twigs, the leaves are nearly uniform in size, similar in colour except a few young ones, and often with 1–2 ageing leaves at the base. Besides, the internodes are nearly equidistant.

(2) In trees with intermittent growth, the leaf-size and the length of internodes are not uniform. At the basal part of the shoot of each season, there are some scars of scale-leaves that protected the young shoot initially.

(3) In trees with intermittent growth, there is usually a sudden change of bark colour, wearing off of epidermis, appearance of cork-layer, lenticels, etc., whereas in continually growing twigs all changes are gradual.

Trees with manifold growth are easily discernible by comparing the branches here and there. Their growth is never continuous, though usually evergreen, and individual branches may be deciduous.

Deciduous trees are very conspicuous at times of leaf-fall. We can find a full account of them in the literature (CORNER '40 and others). The mode of branching has no direct relation to periodic deciduousness.

We shall first examine the mode of branching morphologically and then, combined with the activity of the growing point, the mode of tree-growth in detail.

§ 5. Terminal growth

The terminal growth of trees in the tropics may be grouped into three types, the tuft-trees, the trunked and the ramiferous.

Tuft-trees produce leaves only from their thick stem, as in tree-ferns, cycads, palms, papaya-trees, and they rarely branch. Trunked trees, designated as the monopodial tree, have a main trunk with relatively slender limbs. This form is very abundant in the tropics, not only in gymnosperms, but also in dicotyledonous trees. The ramiferous tree has a short trunk, from which thick limbs subdivide and ramify gradually into slender branches and twigs. Naturally there is no sharp distinction between the latter two. All young dicotyledonous trees grow at first monopodially, but some trees cease sooner or later their terminal growth as their inherent character, though this may be varied more or less by environmental conditions.

The trunked tree sometimes tends to the many-stemmed form near the base, and conversely the ramiferous tree in dense forest may tend to the trunked form up to the high branches.

That there are many monopodial trees in the tropics is one of their characteristics, indicating the favourable conditions of growth. Even in trees with sympodial growth, the pseudo-monopodial form is occasionally seen, as in *Alstonia*. They seem to be suited to dense forest. All these forms are recorded systematically in Corner's book (1940).

Among trees with terminal growth, there are still some distinctions according to whether the organs produced are uniform or not, and how long the apical growth can last. In tree-ferns and most of the palms the kind of organ formed is uniform, while in cycads a set of scales and foliar leaves are produced in each season, so that the growth is intermittent. In the flowering season, then, the female trunk of cycads forms scales, sporophylls and foliar leaves as one set, while on the male trunk, on account of the terminal position of the male cone, the stem-apex, withers and growth proceeds by an axillary bud sympodially. The *Corypha*-palm on the contrary, having formed a terminal inflorescence after about thirty years growth, dies down, while the Sago-palm (*Metroxylon*) succeeds this growth with axillary saplings.

Terminal growth is therefore not necessarily endless. It is a morphological alternative to lateral growth. If the main axis terminates with an inflorescence after some seasons, it is a limited terminal growth, but if the inflorescence is axillary and growth has no morphological limitation, it is an indefinite terminal growth, even if its duration be not very long.

§ 6. Lateral growth

When the growing point dies out or becomes an inflorescence, then one or more lateral buds grow instead and sympodial growth ensues in each season. In some trees, too, chiefly on their horizontal branches, one or more axillary buds of the underside grow more vigorously than the main shoot, which then grows slowly as a short shoot, while the lateral twigs take its place in the continuation of the branch. The same process is repeated in every season, adding new twigs successively. The former two cases may be named "substituting growth" and the latter "apposing growth".

If the growth of lateral buds precedes flowering or dying out of the terminal part, the twig remains evergrowing, but if it falls behind, growth becomes intermittent, though there is no sharp boundary between the two extremes.

1. **Substituting growth**

Two cases may be mentioned, namely the dying of the terminal bud or twig and the fruiting or decaying of the terminal inflorescence. The inflorescence may be represented either by a single flower, an inflorescence, or the anthocladium (GOEBEL '31), e.g. *Delonix,* but as the morphological details are not important, we may call them all inflorescences.

As a typical case of the dying of the terminal bud, *Xanthophyllum Curtisii* may be mentioned. It is an endemic tree of Malaya, growing twice a year intermittently. Though the shoot is provided with green coriaceous leaves, its terminal bud dies every season and an adjoining axillary bud substitutes the growth of the twig (§ 22, Fig. 1). In *Crataeva, Sapium,* and several genera of Leguminosae, a few upper internodes die away and the remaining lower buds develop. The young tree of *Sapium discolor* is especially interesting in respect to its mode of branching. At the end of each season, the apical part of the axis dies away and one of the apparently whorled branches grows upward and takes the place of the main stem. The trunk thus assumes a pseudomonopodial form. Then, after a height of several metres is attained, two branches grow upwards simultaneously, so that the trunk appears pseudo-dichotomous, and these limbs repeat this mode of branching; so in a fairly tall tree a 'dichotomously branched', flat-topped crown develops. In *Alstonia scholaris* a tall pseudo-monopodial trunk grows up and a handsome pagoda form is assumed, as illustrated in Corner's book, Fig. 15.

2. **Apposing growth**

This is the so-called "Terminalia-type branching" (RACIBORSKI '01, p. 50; CORNER '40, p. 30), and involves horizontally spreading branches, such as *Terminalia, Fagraea, Achras,* and *Palaquium,* whether evergreen or deciduous, and occurs even in temperate trees such as *Cornus* and *Idecia.* It is homologous with the rhizomes of *Polygonatum* and many others. In *Tectona* and *Eriobotrya,* when the branches are horizontally directed, the same mode of branching occurs, but growth is usually more or less upwards, and the more upward it is, the more vigorously the main twig grows, tending ultimately to normal ramification. This type of branching is, therefore, a case of geomorphosis caused by hormonal activity in which the branches of the upper side are restricted in their elongation, while those of the underside are accelerated.

So much for the morphology of branching. Let us now consider the growth-forms of trees in general.

§ 7. Evergrowing trees

There are three types of evergrowing trees:—

(1) Shoots are all evergrowing by terminal growth—"the terminal evergrowing".

(2) The shoots show a limited growth by

(*a*) dying of apical parts,

(*b*) development of the inflorescence,

(*c*) tending to be a short shoot,

but the growth is maintained by the development of substituting or apposing twigs without resting.

(3) The shoot-growth is intermittent and sometimes deciduous, but the phase of development is manifold according to branches, so that the tree as a whole is evergrowing (§ 8).

Among the evergrowing trees, we may distinguish further two types: the inherent and the environmental. There are many endemic "evergrowing trees of inherent type". But some trees, though evergrowing in Singapore, are intermittent or deciduous in other regions, so that they may be named "the facultative evergrowing".

For instance, *Duabanga sonneratioides, Thespesia populnea,* and *Trema orientalis* are deciduous in India (TROUP '21) and *Trema* is even bare for 22 days (WRIGHT '05). *Mimosa sepiaria* and *Psidium guajava* are semideciduous in San Paulo and the former is deciduous in Rio Grande do Sul (30° S) (IHERING '23). *Hibiscus tiliaceus* is intermittent in East Java (FABER '35). All these trees are evergrowing in Singapore.

Naturally it is not certain whether the deciduous habit of such trees is environmental or inherent, as there may exist racial differences in each region among widely distributed species (§ 22).

1. The terminal evergrowing

This is the simplest case of the twig-growth. The terminal part of each twig has a constantly growing bud, forming equal-sized leaves one after another, leaving a few ageing leaves behind. The growing point is protected by outer developing leaves, petioles or stipules. Young leaves may have hairy coverings or secrete gum-resin and are more or less sheathing. The hairs are usually simple, occasionally long, branched, tufted or slimy according to species.

Very often the young bud is covered by an outer leaf or a pair of opposite leaves, the margins of which fit together by entangling hairs so as to make a tube or cone. As the inner bud grows, the

connection of the margin is gradually separated and the next leaf, or leaves, restore the arrangement, as in *Duabanga sonneratioides, Horsfieldia brachiata,* and *Campnosperma auriculata.*

The leaves of *Archytaea* and *Gordonia* are glabrous and the young bud is surrounded by the involute leaf-base, or outer leaf respectively, so as to recall the leaf-sheath of *Tradescantia.* When the younger part is protected by the petiole, this is more or less grooved, and in cases of opposite leaves as in Gnetaceae, Apocynaceae, Loganiaceae, etc., the young bud is enclosed between their bases, which often make a tube above the bud filled with an exudation of gum-resin or slime. *Wormia suffruticosa* shows a peculiar form of bud-covering, in which the equitant petiole encloses the bud completely (FABER '35, Fig. 136).

Stipules are often useful for the protection of the bud, too, especially when they are large, as in *Jackia ornata* (CORNER '40, Fig. 190) and *Leea* (LUBBOCK '99, Fig. 188). Trees of Rubiaceae, Polygonaceae, Magnoliaceae, and Moraceae have as well-developed a stipular covering, hood- or cone-shaped, as those of temperate regions. They are described in detail by POTTER ('91), GROOM ('92), LUBBOCK ('99) and others.

a. Tuft-trees

The tree-ferns, most palms and the papaya-tree are the typical monocaulous trees. *Cycas, Pandanus, Dracaena,* etc. are often polycaulous or branched. The growing point develops steadily, deeply protected by a tolerable number of young leaves. Most palms produce inflorescences at the same rate, one by one after the development of the subtending leaf. In the papaya the surface of the growing point is slightly convex and the leaf-primordia are arranged in 2:3 parastichy. In each primordium, there develops at first the columnar petiole with narrow brim-like lamina on the top. The growing point is therefore in direct communication with outer air, though the laminas of older leaves extend horizontally and make a shelter over the young parts.

b. Evergrowing trunk-tree

α. Trunk and branches both evergrowing

Casuarina equisetifolia, Canangium odoratum, Macaranga triloba, Knema malayana, and *Adinandra dumosa* belong to this category. *Adinandra* represents a typical case of the broad-leafed evergrowing tree. The leaves are formed in 2/5-phyllotaxis and both the main axis and lateral branches grow continually, bearing flowers afterwards in their leaf-axils. In *Canangium* most lateral

branches are drooping and, after growing a few metres without thickening and branching, fall away from the abcission layer at the base: they are, so to speak, a kind of short shoot functionally. *Macaranga* is a well known ant-plant (CORNER '40, p. 263). The ants remove with the growth of twigs to the upper internodes successively. It seems difficult for ants, if the branching be sympodial. The South American ant-trees, *Cecropia* and *Triplaris,* are also terminal in their growth.

β. Trees with evergrowing trunk

Glochidion and *Taraktogenus* may be cited. *G. superbum* and others bear on their main axis narrow scale-leaves only, and this main axis grows slowly. In contrast, the lateral branches bear leaves in two rows (CORNER, l.c. Pl. 58). The leaf, or leaves, at the basal part of the twig are small; the next are bigger; and, then, they become smaller again. With further growth of the twig the undulation of the leaf-size is repeated. I observed three such undulations on one twig. This does not however depend on the seasonal change of the climate, as the phase of fluctuation is not the same for all branches. It indicates therefore the very beginning of the rhythmical growth of the twig (§ 10).

γ. Trees with evergrowing lateral branches

Anisophyllea disticha and *Horsfieldia sylvestris* may be mentioned as interesting cases. In *A. disticha* the main axis produces only small leaves, and from this axis 5 lateral branches develop in pseudo-whorled arrangement periodically. The leaves on each branch are arranged spirally in 4 rows, but distinctly anisophyllous with two small upper rows and two large lower rows (CORNER l.c. Pl. 15), just like the shoot of *Selaginella*. That the dicotyledonous tree and *Selaginella* can assume an analogous form is very remarkable. Similar instances are also recorded in Hepaticae, Musci and Podostemonaceae (GOEBEL 28, p. 317).

In contrast another species of *Anisophyllea, A. Griffithii,* bears the usual coriaceous leaves on the twigs. They are apparently alternate, but, on close examination of the young twig, it is seen that the leaves are opposite, but the upper leaf of each node, on account of a strong hypotropous anisophylly, dies away so early in development that one can hardly find its remains.

Horsfieldia is many-stemmed when grown in the open. The main axis of each stem produces in every season (perhaps half a year) ten leaves in 2/5 phyllotaxis, the lower five of which have long internodes but no axillary branches, while the upper five with short internodes produce axillary branches, which bear big leaves of the

same size (35 × 6·5 cm.) in two alternate rows equidistantly (± 2·4 cm.). These branches grow continually without noticeable secondary thickening and branching, so that they hang down gradually, attaining finally 3–5 m., producing small flower-clusters in the leaf-axils or on the branch behind the leaves. These branches are therefore likewise short shoots as in *Canangium* (mentioned above). The branches, though without abscission layer, fall off just like a long compound leaf, lying then sinuously on the ground like snakes.

c. Evergrowing ramiferous trees

This is the most usual type of tree, in which from the trunk large limbs ramify gradually to slender branches and twigs. Such trees are generally monopodial in young stages, but sooner or later the main axis ceases to grow or lateral branches grow vigorously and represent main limbs and branches. Of the evergrowing, ramifying type, there are many, for instance *Campnosperma, Elaeocarpus, Commersonia bartramia,* etc.

2. The evergrowing tree with lateral growth

There are two types of growth, the substituting and the apposing, as already mentioned.

a. The substituting growth behind the inflorescence

The flowering of the terminal inflorescence is either seasonal, contemporary or non-seasonal according to species, but new shoots can be seen throughout the year.

In the seasonally flowering trees of evergrowing type, the season is once or twice every year according to species. As once-flowering trees may be named *Parkia speciosa, Cassia nodosa,* and *C. siamea.* In the last named, the growth of branches is tolerably irregular and the flowering continues from May to October according to branches, so that it seems rather manifold or represents a transitional case to it. Perhaps the species originated in the monsoon region and is tending to everflowering in Singapore.

As twice-flowering trees, there are *Ervatamia dichotoma, Albizza falcata, Enterolobium saman,* and *Cassia multijuga,* among which the last named *Cassia* is also irregular in the branch-growth and its flowering continues for three months every season.

Among the contemporary flowering trees, there are shrubby *Coffea* spp. and *Stenolobium stans.* The latter flowers several times every year gregariously, stimulated probably by the temperature-fall, as in *Coffea.* The irregularly branched raceme contains flower-buds of various ages (CORNER l.c. Fig. 44) and only the older

buds react to the stimulus, while younger ones wait for the next chance. New lateral shoots grow all the time irregularly.

As trees of non-seasonal flowering, there are *Cerbera, Ochrosia, Kopsia, Plumeria, Ixora, Vitex* and others. The flowering is more conspicuous twice every year, but the flowering can be seen at any time, so that it seems to be transitional to manifold growth and flowering. This is especially the case in *Kopsia* and *Plumeria. Wormia suffruticosa* has continual substituting growth. The inflorescence is terminal at every node, but the axillary vegetative bud grows early and assumes the terminal position, so that the inflorescence seems opposite to the subtending leaf. *Jatropha multijuga* has the same mode of growth.

b. Apposing growth

Fagræa fragrans grows luxuriously in Singapore with a handsome crown and is well adapted to the soil-conditions. It is originally monopodial, but in open ground develops often "subtrunks" with big limbs. They branch in *Terminalia*-fashion and are evergrowing. Each short shoot produces one pair of opposite leaves every two months, and counting from the number of leaf-scars, each short shoot dies away after about 6–7 years, but new shoots are added one by one laterally, extending the branches outwards. Flowers in axillary clusters are conspicuous in May and October (§ 12). *F. gigantea* also shows apposing growth in the same fashion.

Apposing growth is not confined to evergrowing trees, but occurs also in trees of manifold and intermittent growth, some of which are deciduous, as mentioned below:—

Manifold: *Achras Zapota, Palaquium gutta;*

Intermittent: *Pterocymbium tinctorium, Terminalia Muelleri;*

Deciduous: *Sterculia macrophylla, Firmiana fulgens.*

§ 8. Trees with branches of manifold growth

So long as a tree shows continuous growth, there is no manifold growing. In lateral-growing trees, if the development of axillary buds occurs in every branch non-seasonally, it may be regarded as a manifold growth in short steps. In typical manifold-growing trees, however, whether the growth is terminal or lateral, one can discern the growing and resting branches, or the vegetative and flowering branches at a glance. This is seen very often in sympodially growing trees, because even a slight difference of the development phase of new shoots behind the dying twig or inflorescence exerts a further shift of growth and this affects the growing phase and emphasizes the individual differences more and more.

This is the usual case of manifold growth accompanied by lateral branching. But there are still two other cases of the manifold growth. The one is the big tree in general. As a tree grows taller, the light-condition, the ascent of sap, etc., become uneven according to the position of the branches, and, so far as the climate is uniform, exerting no seasonal restriction, each branch may submit to a position effect and the result tends to be manifold.

As the second case, various exotic trees may be named. Most of them are adapted inherently to the dry or cold season with intermittent growth, and even under the uniform climate the tendency does not disappear so easily in each twig. By a combination of twig-individuality and position-effect, the manifold growth is emphasized. This is not only the case in the warm region, but observed also in the cool alpine region with uniform climate. For instance, temperate trees as *Magnolia, Pyrus* and others, transplanted to the Alpine Garden of Tjibodas (1425 m) of Java, show similar manifold growth (HABERLANDT '93, SCHIMPER '98, FABER '35). I have observed also these features in that Garden, as well as on the summit of Mt. Tankoeban Prahoe (2076 m), where *Vaccinium varingiifolium* shows typical manifoldness remarkably.

So far concerns the branchwise manifold growth. As to the stockwise manifold growth, it is very common in transplanted trees, e.g. *Lagerstrœmia flos-reginæ, Cassia fistula, Delonix regia, Spathodea campanulata, Hevea brasiliensis* and various other avenue trees. Perhaps at the time of transplanting of nursery trees, a slight difference in treatment, as the cutting away of branches and roots, affects the further growth of the young trees, and, as there is no climatic restriction, each tree or branch take its own way and manifold growth follows gradually.

1. **Terminal manifold growth**

This is observed in intermittently growing trees and there are transitions from nearly evergrowing to deciduous, e.g. *Myristica fragrans, Eugenia aromatica, Michelia alba, Carapa guianensis* and some genera of Leguminosae.

Myristica seems at a glance to be evergrowing, but really intermittent in a slight degree. In the Moluccas, its native district, the fruit-season is once every year, so the tree in Singapore seems to be converted to manifold growth of nearly evergrowing habit. The axillary flowers develop in ascending order one by one and the fruits of various size are seen in various positions on twigs here and there. For *Eugenia aromatica* the condition seems almost the same, though no flower is seen.

Michelia alba is of continental origin and in the north and middle part of Malaya it is more or less deciduous (CORNER, l.c. p. 434), but in Singapore it is evergreen and manifold. Both the resting and growing bud are covered by the characteristic scale-like stipules of the family. It grows twice every year vigorously, but new shoots can be seen throughout the year with fragrant white flowers, more abundant in some stocks than others.

Carapa guianensis produces brown or light green new shoots here and there over the dark green crown. The resting buds are covered densely by ten or more scale-like petioles even in Singapore. In Ceara (4° S), Brazil, the tree is deciduous (IHERING '23).

Amherstia, Brownea and *Saraca* show the most conspicuous manifold growth represented by new, white or brown, hanging shoots mingled with the green crown. Besides, some conifers, such as *Pinus Massoniana, P. Merkusii* and others, also grow manifoldly in Singapore.

2. **Lateral manifold growth**

a. Substitution of the withered apical part

In some trees one or more apical buds of twigs wither after producing a certain number of leaves. New shoots then arise from the buds of the proximal part and substitute with their new growth. The withering has no intimate relation with the season, so that the new growth becomes manifold. *Crataeva Roxburghii, Semecarpus sinensis, Pistacia formosana,* and *Sapium sebiferum* (deciduous in China) are instances.

b. Substitution of the inflorescence

Tectona grandis grows well in Burma, East Java and other monsoon regions and is deciduous, while in Singapore it tends to be evergreen, though the growth is poor. The development of the shoot is extremely manifold, forming the terminal inflorescence non-seasonally. *Crataeva* (mentioned above) also forms a terminal inflorescence sporadically.

c. Apposing growth

Achras zapota is, though evergreen, distinctly intermittent in the growth of its successive short shoots. The resting bud is covered by petiolar scales and the growth of twigs is fairly manifold, so that the ripening of axillary fruit is non-seasonal. *Palaquium gutta* of the same family shows a similar mode of growth, though nearly evergrowing.

d. Stockwise manifold growth

The leafing, flowering or leaf-fall of each stock proceeds in this case with different phase, indicating that the climatic influence is rather ineffective for periodicity. This is especially noticeable in avenue trees with attractive flowers or young foliage. *Lagerstroemia flos-reginae, Cassia fistula, Peltophorum pterocarpum, Delonix regia,* and young trees of *Spathodea campanulata* give to travellers an impression, that the tropics is the land of everflowering. The bright-red foliage of *Cinnamomum iners* is likewise striking.

The flowering season of *Cycas Rumphii* is also stockwise manifold and, as it is dioecious, the pollination may sometimes be missed, when the trees are not abundant.

§ 9. Intermittent growth

In this case the unfolding of new leaves occurs periodically every year once or more, and full-grown shoots show a fluctuation in the size of leaves as well as in the length of internode, with resting buds on the apex and in the axils. The mode of branching, terminal or lateral, has no direct connection with the periodicity. As trees of terminally intermittent growth, there are *Kurrimia paniculata, Quercus conocarpa, Durio zibethinus,* and as the substitutingly intermittent ones *Xanthophyllum Curtisii* and *Cleistanthus heterophyllus.* Those with intermittently apposing growth have been stated already (§ 7–2–b).

For the covering of resting buds in the tropics, there are various modes and grades. Some are nearly naked as in the growing bud, but others are covered tightly by scales derived from the petiole, stipules or modified leaf-base or blade.

The axillary buds are usually in the resting condition. They are sometimes naked, sometimes covered by a pair of prophylls. This is also the case in the evergrowing trees (§ 22).

New foliage is usually light green, sometimes brownish red or even blue (CORNER, l.c. p. 85), and often more attractive than the flower. When strolling in the forest, one will notice very often, that many trees are in new leaf gregariously. This appearance is very common after a dry spell of several days, but one can see at any time new leafing here and there, denoting that new leafing is induced either by the weather condition or by the internal activity, facultatively or by a combination of both.

In trees with intermittent growth, therefore, there are three types of the leafing: the seasonal, the contemporary and the non-seasonal. In the seasonal leafing the frequency is 1–3 times every year, twice being the most usual in Singapore. Contemporary leafing is not regular in calendar months, and occurs in accordance

with a slight change of the weather. Non-seasonal leafing is much more irregular. Some instances of leafing are as follows (Roman number denotes the month):—

(*a*) Seasonal leafing: once every year: *Emblica officinalis* (III), *Parkia speciosa* (III), *Erythrina lithosperma* (X); Twice a year, chiefly in February to March and August to September after the dry spell: *Kurrimia paniculata, Castanopsis* and *Quercus* spp., *Calophyllum inophyllum, Garcinia mangostana, Parinarium corymbosum, Nephelium lappaceum, Gordonia* spp.; thrice a year: *Eugenia grandis* (III, VII, XII).

(*b*) Contemporary leafing: *Flacourtia rukam* (3 times), *Cinnamomum iners* (3–4 times), *Rhodamnia trinervia* (4–5 times). In *Cinnamomum* one can see, besides the usual contemporary leafing, sporadic leafing according to stocks at any time of year, or the non-seasonal leafing is here more or less combined. In *Rhodamnia* the leafing as well as the flowering in the same district is simultaneous, but the leafing and flowering do not necessarily coincide. Probably flowering is caused by a sudden fall of temperature, while the leafing is induced after a dry spell of weather.

(*c*) Non-seasonal leafing: *Mangifera foetida* (less than one year) and many trees with non-seasonal leaf-fall.

§ 10. The transition from the evergrowing to the intermittent

In the tree-growth of the tropics, there are various transitions from the evergrowing to the intermittent and, further, to the deciduous (§ 11 and 22). The first indication of intermittent growth developing from evergrowing is fluctuation of leaf-size. *Bridelia tomentosa* grows continually in its main stem, and the lateral branches bear leaves in two rows alternately. But the leaves are not of uniform size, the spray showing a more or less waved outline as a whole. In long branches one can see three such waves representing three periods of growth. The leaf-size is larger in the middle part and smaller (ca. $\frac{1}{2}$ in size) in the proximal and distal parts of each period with shorter internodes. *Glochidion* of the same family shows likewise a fluctuation of the leaf-size, though it is more or less disturbed when secondary branches appear. Some conifers, such as *Araucaria Bidwillii, Dacrydium elatum* and one variety of *Cryptomeria japonica* (var. *araucarioides*), also show this fluctuation.

With further advance of the periodic tendency, a few proximal leaves of each season wrap up the inner part of the shoot, and fall off after development of the latter. For instance in *Rheedia madruno,* one or two leaves, though green, are merely 1/5 of the normal length. In *Gordonia singaporeana* the first leaf of each season is small, light green and falls early. The second leaf is also a little smaller than usual, brownish-green in colour containing anthocyan, falling likewise early, and from the third leaf onwards the normal form is assumed. In *Myristica fragrans* the resting bud is naked and the proximal two leaves embrace each other, protecting the inner leaves, and fall early after elongation of the shoot.

With still further development of the intermittent tendency, the growing point becomes a resting bud, formed after the production of a number of leaves, initiated by primordia as incomplete coverings, or well-developed scales, wrapping a number of younger leaves. The bud-envelope is represented sometimes by incomplete leaves, at other times only by petioles or stipules without blade. When the petiole serves as the covering, the lamina does not develop well (*Achras zapota*). When the leaf is sessile, the covering may change gradually from scales to the normal leaf (*Lucuma*), and, in the cases of the stipulate leaf, the entire leaf-element may form at first a scale (*Aporosa nigricans*), or at first only stipules are formed and then, after forming some prophylls, the foliar leaves develop abruptly (*Kurrimia paniculata*) or with gradual transition (*Brassaia actinophylla*).

How shall we then define the intermittent growth in contrast to the evergrowing, as they are only of gradual change in nature? It seems, however, adequate to define the shoot as evergrowing, when leaves at the onset of the new shoot, even if small in size, remain as assimilating leaves, as in *Bridelia* and *Rheedia.* But, if the leaves, even if green, are distinctly small and fall off early (*Myristica*) or show a difference in size and colour (*Gordonia*), one may define the shoot-growth as intermittent. Such a rhythmic character of the shoot is quite independent of climatic changes and is undoubtly caused by inherent hormonal activity on the growing point, by which the formation, growth and senescence proceed periodically, often with a pre-determined number of leaves (§ 23).

KLEBS ('15) once claimed that the periodicity of tree-growth could be controlled artificially. But the continual growth of trees is seen only in evergrowing trees or saplings, which latter tend then to rhythmic growth. The opinion that the supply of minerals may cause the evergrowing or intermittent growth is also inconceivable, as in so uniform a climate as Singapore both types of tree, the

evergrowing and intermittent, flourish side by side, and also stockwise manifold growth occurs. At any rate, the basic cause is the inherent factor, by which the trend to periodicity is determined.

§ 11. Deciduous trees

In evergreen trees with intermittent growth, the older leaves fall off after new leafing. But there are trees in which leaf-shedding precedes new leafing, exposing thus naked branches, and thereby characterising the deciduous tree. In them three phases of development, leaf-fall, naked branches and new leafing, follow successively. The mode of branching is not intimately related, whether it is the terminal (*Ficus, Hevea*), the substituting (*Cassia fistula, Lagerstromia* spp., *Sapium discolor*) or the apposing growth (*Terminalia catappa, Sterculia macrophylla*).

The naked phase is usually not very long in the tropics, though flowering or fruiting may even proceed during this spell, e.g. *Parishia insignis, Cratoxylon formosum, Firmiana fulgens, Parkia javanica, Cochlospermum religiosum,* and *Oroxylum indicum.* In regions with a long dry spell, the number of such flowering trees increases much more (TROUP '21).

1. Transition from the intermittent evergreen to the deciduous

In Singapore the resting period of trees is rather short and sometimes indistinct. Usually the spell is one week or so, rarely a few days only. Moreover there are some trees, in which new leafing begins before leaf-fall has finished. Various irregularities occur too.

As an instance, a para-rubber tree in the Botanic Gardens showed in March, 1944, from the top downwards, a transition of new foliage, naked branches, tinted leaves and old green leaves, and in April of the next year the same nuance of phases. The tree took for the leaf-change of the entire crown nearly three months.

Swietenia macrophylla from Central America is, so to speak, a deciduous tree, but most avenue trees of it have emitted new brown shoots by the time the old leaves are falling off. *Dyera costulata* is deciduous, but I saw once on a big tree in the Gardens that the old leaves remained on a few of the lowest limbs until the next period of leaf-change. Trees tend in general to be more irregular in their periodicity, the bigger they grow.

Thus the transition from the deciduous to the intermittent-evergreen may be classified in four stages:—

(1) Holodeciduous: entire crown becomes bare at least for a few days: *Peltophorum pterocarpum.*

(2) Semideciduous: new and old foliage, as well as naked branches, appear irregularly according to the height, direction, etc. of branches: *Hevea brasiliensis.*

(3) Vice-deciduous: leaf-fall is finished during one week promptly, but new shoots appear before old leaves fall off completely: *Swietenia macrophylla.*

(4) Semi-evergreen: some branches do not shed leaves till next season, tending to be intermittent-evergreen: *Dyera costulata.*

Naturally these grades of the leaf-fall are not absolutely constant, and may be shifted according to year or district. Deciduous trees of N. Malaya can easily become semi-deciduous in Singapore, if the season is not sufficiently dry.

Both the leaf-fall and new leafing occur in most trees nearly simultaneously, but in some the leaf-fall proceeds gradually for 2–4 months, while the new leafing occurs at once, as in *Sapium discolor* and *Terminalia subspathulata.* These cases indicate that the new leafing does not necessarily follow on the formation of the abscission layer of old leaves. Both of them are independent processes (§ 18) and, if the former occurs earlier than the latter, the tree is evergreen, while it is deciduous when the former is delayed.

2. The leaf-period and the date of leaf-fall and leafing

The duration of the leaf-bearing period of deciduous trees in Singapore is three months to more than two years. They may be seasonal or non-seasonal, and the latter may be contemporary.

Seasonal leafing or leaf-fall is in most cases once or twice in a year, chiefly after a dry spell, rarely thrice. Non-seasonal leafing is sometimes shorter than one year and sometimes longer according to species. We may designate them as the "shorter" and "longer" leaf-period of deciduous trees respectively.

(*a*) The average date of leafing of seasonally deciduous trees (The names in brackets indicate exotic trees: e: early, m: middle, and l: later part of the month given in Roman numerals) (HOLTTUM '40, CORNER '40).

(1) Once every year		(2) Twice every year	
(*Canarium rufum*)	.. V, e	(*Couroupita guianensis*)	15/III, 20/IX
(*Cariniana* sp.)	.. VIII, m	*Elateriospermum tapos*	.. I, VII–VIII
(*Hymenaea courbaril*)	.. II	*Peltophorum pterocarpum*	12/II, 10/VIII
(*Kigelia pinnata*)	.. I, l	(*Pentaspadon officinale*)	III–V, X–XI
Parkia javanica	.. II, l	*Terminalia catappa*	.. 2/II, 11/VIII
Terminalia subspathulata	.. IV, e	(3) Thrice every year	
		Ficus caulocarpa	.. I, l; VII, e; XI, e

(*b*) The mean leaf-period of the non-seasonal deciduous trees (HOLTTUM, l.c.).

(1) Shorter Period	Months	(2) Longer Period	Months
Ficus variegata	6.1–6.5	(*Hevea brasiliensis*) ..	13.3
Sterculia macrophylla ..	6.9–7.0	(*Homalium graniflorum*) ..	13.7
Adenanthera pavonina ..	7.25	*Anisoptera megistocarpa* ..	13.8
(*Delonix regia*)	8.8	*Cedrela glaziovi* ..	14.0
Cratoxylon formosum ..	9.1	*Caesalpinia ferrea* ..	14.2
Lagerstroemia flos-reginae ..	8.1–9.4	*Parishia Maingayi* ..	15.6
Cassia fistula	9.1–10.5	*Heritiera elata* ..	20.5
(*Salmalia malabarica*) ..	9.3–10.5	(*H. macrophylla*)	26–37
Cassia nodosa	11.7		

§ 12. The flowering season

The flowering season may similarly be arranged into four groups: continuous, seasonal, contemporary and non-seasonal.

Continuous flowering follows as a natural sequence in some evergrowing trees, in the leaf-axils of which the flower buds are formed, though evergrowing trees are not necessarily everflowering. Seasonal flowering takes place 1–3 times every year according to species, and in definite season. Contemporary flowering occurs, though not at a definite season, in all trees of a species in the same district simultaneously. Non-seasonal flowering is indefinite in the calendar year and can vary by branches and stocks according to species, so that branchwise and stockwise manifoldness appear.

Flowering occurs sometimes in consequence of the development of new shoots, on which the flower is afterwards formed. This is especially the case with the terminal inflorescence of the shoot of each season. But in trees with axillary, ramiflorus, or cauliflorous flowers no such relation exists or climatic conditions are the chief cause.

Among trees with evergrowing shoots, about half flower continuously, while the rest are either seasonal, contemporary or non-seasonal. Most manifoldly growing trees are also non-seasonal in flowering, but some are seasonal in relation to the climate. Among intermittently growing trees, the seasonal leafing shoot is also seasonal in flowering, and on the non-seasonal leafing shoot follows generally the non-seasonal flowering, too.

1. **The flowering of evergrowing trees**

Evergrowing trees are not all everflowering. If the flowers are formed in the axils of twigs and open successively, they are everflowering. But if the flowering is controlled by the weather, it may tend to seasonal or contemporary flowering. If the shoot growth is substituting and the inflorescence is terminal, the flowering may become seasonless according to the shoot growth. And when the formation of flower buds is sporadic, as in the lateral branches of *Anisophyllea disticha,* so the flowering is optional or non-seasonal, even if the branches grow continuously. The following instances are the chief cases of flowering types of the evergrowing trees:—

(*a*) Everflowering: *Carica papaya, Adinandra dumosa, Archytaea Vahlii, Commersonia bartramia, Glochidion* spp., *Macaranga* spp., *Hibiscus* spp., *Thespesia populnea, Scaevola frutescens, Sesbania grandiflora, Leucaena glauca, Mimosa sepiaria, Solanum Wrightii, Symplocos fasciculata, Wormia suffruticosa, Psidium guajava, Melastoma malabathricum.*

(*b*) Seasonal flowering: Twice a year: *Casuarina* spp., *Fagraea fragrans, Artocarpus, Morinda, Gardenia, Horsfieldia.* Once a year: *Hydnocarpus, Elaeocarpus* spp.

(*c*) Contemporary flowering: *Stenolobium, Coffea,* some Orchids.

(*d*) Non-seasonal flowering: *Arthrophyllum, Bridelia, Canangium, Leea, Mallotus, Rhizophora.*

2. **Seasonal flowering**

This is intimately correlated with the climatic course, but two cases must be distinguished. The one is that in which the leafing is associated with the season, so that the flowering occurs as a consequence also seasonally. The other is that the flowering is induced directly by the seasonal change, independent of the leafing. To the former belong the evergreen, the intermittent and the deciduous trees either with the terminal or axillary inflorescence, and to the latter the evergrowing and intermittent-growing trees with either terminal, axillary or cauline flowers. Some instances are tabulated below. The number in brackets indicates the frequency of flowering in every year.

a. Seasonally leafing tree

Flower terminal: deciduous—*Peltophorum pterocarpum* (2).

Flower axillary { evergreen { *Eugenia grandis* (3). *Garcinia mangostana* (2). ; deciduous—*Terminalia catappa* (2).

b. Seasonally flowering tree

Flower terminal—*Fagraea auriculata* (1).

Flower axillary—*Fagraea fragrans* (2), *Casuarina* spp. (2), *Erythrina subumbrans* (1).

Flower ramiflorous—*Horsfieldia sylvestris* (2).

Flower cauliflorus—*Durio zibethinus* (2).

Casuarina equisetifolia is distributed from Australia to the eastern coast of India, adapted to typical monsoon regions. So, even under evergrowing conditions in Singapore, it shows two flowering seasons, probably as a specific character. The flowering of *Fagræa fragrans* is however a little different. The flower-buds are formed in the dry spells of February and July and open in May and October. The flowering is especially conspicuous in May (HOLTTUM '35), but it fluctuates more or less according to the year. For instance, in February, 1945, it was rainy and a short spell of rainless days came in April, so that most trees were seen in flower July to August. In big trees, however, some branches flowered in May tending to be slightly manifold. Besides, some young trees flowered in March or in December of the previous year; thus even a stock-wise difference was noticed. For the anthogenesis of *Fagraea* there is necessary, therefore, the timely co-operation of the internal tendency with the external climatic course.

Generally, if the formation of flower-buds is controlled by weather and in one season the weather is not effective enough, so the trees can not react uniformly all together. In some stocks or branches the bud-formation can diminish or not occur. Then this irregularity can exert a compensatory after-effect at the next season, so that even seasonal flowering tends to be seasonless or manifold.

3. **Contemporary flowering**

In this case the young buds formed can not flower right away; they rest in a certain stage of development, waiting for the sudden fall of temperature by a shower, by which they are stimulated to grow anew, and after a certain number of days all flowers of the district open gregariously. They are called the temperature-flowers (CORNER, l.c.p. 38).

The most conspicuous gregarious flowering was studied with *Dendrobium crumenatum,* an epiphytic orchid, in detail (COSTER '26, KUIJPER '33). Among trees and shrubs, *Pterocarpus indicus, Murraya paniculata, Randia macrantha, Stenolobium stans,* and *Coffea* spp. may be named (HOLTTUM '40, CORNER '40). The inflorescence of *Pterocarpus* follows on the new leaf-growth;

the buds are formed in successive stages of development, and the old buds react to the temperature fall, while the younger ones wait for the coming chance, so that the flowering of an inflorescence is divided into several stages with pauses of a few days or more. The flowering of *Pterocarpus tinctorius* of Africa is also divided into four periods (v. NOLDE '40). *Stenolobium stans* forms the inflorescence throughout the year and one can see gregarious flowering about ten times every year. Besides, *Flacourtia rukam* shows 2–3 times and *Rhodamnia trinervia* 4–5 times, flowering and fruiting.

4. **Non-seasonal flowering**

This is seen in shoots and stocks of manifold growth with the inflorescence either terminal, axillary or ramiflorous.

a. Branch-growth manifold

Inflorescence { terminal—*Cassia splendens, Vitex, Kopsia, Ixora.*
axillary—*Michelia.*

b. Stock-growth manifold

Inflorescence terminal—*Lagerstroemia flos-reginae.*

Anthocladium terminal—*Delonix regia.*

Inflorescence ramiflorous—*Cassia fistula.*

Branch and stockgrowth manifold—inflorescence terminal—*Spathodea.*

The shoot of *Kopsia* produces a terminal inflorescence after some pairs of leaves are formed, and, while the flower-buds are still young, the lateral branches grow out to a tolerable size. This mode of growth is repeated irrespective of the season, so that both the flowering and the shoot-growth go on non-seasonally together. In *K. singapurensis,* though the flowering season predominates in two seasons every year, yet one can see some flowers at any time, and in *K. fruticosa* the flowers are seen throughout the year. *Thevetia, Ochrosia* and *Cerbera* of the same family, and *Ixora* and *Vitex* show similar behaviour.

Spathodea produces a terminal inflorescence on each substituting new shoot, and each inflorescence bears scores of buds opening successively, so that old trees are decorated with big flame-red flowers all over the crown the year round.

Among the four groups just mentioned, the everflowering and the non-seasonal ones are controlled inherently, while the contemporary and seasonal ones, though inherent originally, are actually induced at the last step by some trifling change of the weather.

In the humid region of the temperate zone, the formation of flower-buds is controlled generally by the temperature and photoperiod, and in trees it is induced chiefly by the seasonal change of temperature, while a dry spell, even if it may affect the abundance of flowers, does not control anthogenesis. In Singapore, on the contrary, there is no seasonal change of temperature and photoperiod, but the length of the dry spell, accompanied by intensified insolation and thermoperiod, and the sudden fall of temperature during a shower are the chief meteorological conditions. Some species of trees are sensitive to such slight weather changes for their anthogenesis.

§ 13. The fruiting season

The ripening of fruit after flowering takes usually 2–5 months according to the species. In some cases flowering is the morphological sequence of the leafing, but in others not. In the former case, leafing, flowering and fruiting are three consecutive processes, while in the latter the season of fruiting is subject only to the flowering. But the ripening of fruits is sometimes affected by their position on the branches or the inflorescence. For instance, the raceme of *Adenanthera pavonina* develops soon after the leafing of every seven months period (§ 11–2), and it flowers gradually during two months, but the ripening of pods continues for several months, so that the glossy red seeds are dispersed nearly throughout the year.

In Singapore anthogenesis is induced chiefly in the dry spells of February and July; the flowering follows two months later, and the fruiting is most abundant in June to July and January. This is remarkable in durian, mangosteen and rambutan, though one and the same tree does not produce every season regularly. According to OCHSE ('31), these fruits appear in Java only once every year with longer duration than in Singapore.

The fruiting season of the everflowering *Averrhoa* and *Psidium* and of the manifoldly flowering *Achras* is extremely long, so to speak nearly non-seasonal, though with fluctuation. *Flacourtia rukam* fruits 2–3 times contemporarily. *Papaya, Musa* and *Ananas* show stockwise manifoldness of fruiting, so that they serve as good table-fruits throughout the year.

§ 14. The frequency of species in the four types of periodicity

The number of species I could examine personally or extract from the literature (RIDLEY '22–24, CORNER '40) amount to 543, belonging to 298 (211 + 87 exotic) genera and 73 families (after ENGLER's system). There are still 13 other families in Malaya containing trees, which I could not investigate.* *Achras, Aleurites, Anacardium, Anona, Carica, Ceiba, Delonix, Hevea, Jatropha, Leucaena, Muntingia, Plumiera, Psidium, Sesbania, Spathodea, Thevetia* and others are included as exotic genera. Under the exotic species observed, those that are not common in Malaya are all those planted in the Botanic Gardens, Singapore. Among exotic trees enumerated in the Appendix, there are four families not indigenous to Malaya, namely Salicaceae, Bixaceae, Papayaceae and Cactaceae. Besides, there are some families or genera in which only exotic species are treated, though the families or genera themselves are indigenous to Malaya, as Pittosporaceae, Polygonaceae, Proteaceae, Solanaceae, Thymeliaceae, as well as various genera.

Naturally there is no boundary between shrub and tree, and there are many shrubs that grow continually just like young trees, but shrubs as *Lantana* and *Ardisia* are omitted from the list, as there are many trees in these families, while big evergrowing shrubs of Goodeniaceae, Solanaceae and Asclepiadaceae are added.

Among the Malayan families, those containing evergrowing trees amount to 35, or nearly the half of the total families examined. Families containing deciduous trees amount to 32, or about the same as those of the evergrowing ones. Compared with them, the families containing intermittently growing trees are the most abundant, namely 48, or including the exotic families 52. The number of species in each group was as follows (exotic species added in brackets), though sharp boundaries between the growth-forms do not exist:—

evergrowing	manifold	intermittent	deciduous
103 (46)	14 (26)	154 (60)	108 (31)

It may be remarked, however, that the deciduous trees are all easily noticeable in contrast with the evergrowing trees, while the latter are not distinguishable unless actually examined, so that the number of the latter given above seems distinctly less than the actual rate. Concerning the intermittently growing trees, as the writer observed only a few species of the genera which contain

* Gonystylaceae, Staphyleaceae, Sabiaceae, Samydaceae, Styraceae, Acanthaceae, Caprifoliaceae, Crypteroniaceae, Cunoniaceae, Epacridaceae, Monimiaceae, Hermandiaceae, Opiliaceae.

many similar species, the number given above is also distinctly less than the actual rate. The manifoldly growing trees are much more numerous in exotic species than in the Malayan (26:14).

At any rate it may be asserted that among all tree-species of Malaya the evergrowing trees, even with the addition of Palmaceae, Coniferae and tree-ferns, amount to less than 20 per cent, probably 15 per cent. The deciduous trees total about 5 per cent over the whole Malay Peninsula, though some of them do not shed leaves in Singapore. The remaining 75 per cent are the usual evergreen trees with intermittent growth.

In Java, according to KOORDERS ('98) the deciduous trees amount to about 5 per cent among indigenous ones, distributed chiefly in the eastern and middle Java (FABER '35, p. 374). In Ceylon according to WRIGHT ('05, p. 463), deciduous trees make about 14 per cent among 650 indigenous species and 6 per cent (17 species) among endemic species.

The occurrence of deciduous trees in dicotyledonous families is fairly even, just like the evergrowing trees, being more abundant in big families (see Appendix).

How such a circumstance has been derived, is a thesis to be discussed further. If one observes the deciduous trees more closely, they are not all mesophytic; there are even hygrophilous-deciduous trees living in swampy ground, and contrarily there are some hygrophobic trees unable to grow in as wet a district as Singapore. From these facts, the interrelation of the deciduous trees and the environment seems much more indirect.

§ 15. Comparison of the leaf-fall and leafing periods of Singapore with those of Ceylon and Java

So far we have dealt with the behaviour of tree-growth in Singapore and Malaya. Now, if we compare its features with those of Ceylon and Java, it is very instructive to discover what characters of periodicity are easily affected by external influences. The most remarkable difference among the deciduous trees in these three regions is the calendar data of the leafing related to the monsoon.

From India to Indo-China the rainy season extends from May to October, especially rainy from June to September, and the dry season in winter from November to April. Temperature is relatively low in the first part of the dry season from December to January, while it is very hot from March to May on account of fine weather, but then, despite the sun's higher position, it gets cooler on account of the cloudy sky (WRIGHT '94, TROUP '21, CHAMPION '36). These changes of seasonal climate deviate naturally

with the distance and direction of the ocean as well as the mountain range. For instance in Ceylon, the south-west monsoon predominates from February to July and the north-east monsoon from August to January, so that the seasonal change is three months earlier, and moreover it differs according to the south-western side and north-eastern side of the island (WRIGHT l.c.). But as a whole, the general feature of the seasonal change in S.E. Asia is as mentioned above.

In India the deciduous trees of northern origin shed their leaves usually during the winter, those of southern origin mainly in the second half of the dry season, indicating the hereditary habit of their birth-place. In Peradeniya (473 m.) February is the most rainless and dryest season, and about half of the deciduous trees (47 per cent) shed their leaves in this month; before and after that month the proportion decreases gradually until in the rainy season of September it attains the minimum (2 per cent) (WRIGHT, l.c.).

In Buitenzorg the monthly mean maximum temperature is 29°–31° and the mean minimum 21°–22·5°, so that there is no veritable seasonal effect on the growth of the plant (SCHWEIZER '32). Of the rain-fall, however, there is a notable fluctuation, though it is sufficient all over the year. From July to September the mean monthly rain-fall amounts to 135 mm., while in October it is 706 mm. On the other hand, in Soemaran, Middle Java, while in February the rain-fall amounts to 300 mm., in July to August it is less than 10 mm., and eastwards it diminishes more. In Pasoeruan, East Java, from August to September the mean rain-fall amounts to a few millimetres only (COSTER '23). Eastwards in Lesser Sunda Islands it diminishes more and more, with a longer dry spell, so that it tends to be the typical monsoon climate (RENSCH '30).

Thus the dry and rainy seasons are in Ceylon and Java diametrically opposite, while in Singapore, situated in the intermediate region, the climate is mild and non-seasonal. It is instructive therefore to compare the leaf-period of these three regions.

The leaf-period of various trees has been reported in India, Ceylon and Burma by WRIGHT ('94), TROUP ('21), STAMP ('25), CHAMPION ('36), in Java by VOLKENS ('12), SIMON ('14), COSTER ('23), and in Singapore by HOLTTUM ('31, '40), CORNER ('40) and others. If we compare the leafing period or the leaf-fall season of some deciduous trees reported commonly in these regions, we can find a striking contrast between them, as has been stated by many authors already.

TABLE 5

The leafing or leaf-fall period in Singapore, Ceylon and Java after HOLTTUM, COSTER and WRIGHT, l.c. (Month in Roman number).

Trees	SINGAPORE		CEYLON		EAST JAVA
	leaf-period (months)		leaf-fall period	bare days	leaf-fall period
Adenanthera pavonina ..	7.25	(6.0–8.5)	X–XII	30	——
Delonix regia ..	8.8	(7.7–10.6)	IV–V	——	VIII–X
Lagerstroemia flos-reginae	9.2	(8.9–9.4)	XII–I	27	——
Salmalia malabarica ..	9.9	(9.3–10.5)	XII–I	ca. 3 months	VII–X
Cassia fistula	10.6	(9.1–10.5)	II–III	18	VIII–X
„ *nodosa* ..	11.7	(11.0–12.1)	I–III	——	V–VII
Tamarindus indica ..	12.9	(10.0–17.7)	III–IV	——	VIII–XI

These trees in Singapore are, except *Tamarindus,* in their leaf-period all shorter than one year, while in other districts the leaf-fall is one year regularly with a shift of nearly half a year in the leaf-fall season. According to these data, the difference of climate has two effects on the periodicity—the shifting of the period as well as the leaf-duration. In other words, the active period of the tree-growth is transformed rather flexibly by environmental conditions. This is also the case with the grade of leaf-fall (§ 16), while the bud-forming ability, as we will see later (§ 23), is rather constant.

The vegetative period seems, therefore, the most easily movable character of trees in accordance with the change of climatic cycle. According to WRIGHT ('05, p. 7) the flowering season of *Acacia dealbata,* indigenous to south-eastern Australia, has been entirely shifted following the climatic cycle in the Nilgiris in India. It flowered from 1845 to 1850 in October just as in Australia, but then the flowering season was gradually advanced, in 1860 to September, in 1870 to August, in 1878 to July and lastly in 1882 to June, just the spring season of the new habitat. It took about forty years for the seasonal acclimatization. Whether a tree is able to acclimatize by lengthening the active period, the writer could not find a suitable example, though it seems not impossible according to the circumstances. In the trees mentioned in Table 5

(above), it is not known in what sequence they have had their active period transformed.

In non-seasonally leafing trees in Singapore, some are shorter and others longer than one year in their leaf-period (§ 11–2). *Cratoxylon formosum* in Singapore has a leaf-period of 9·1 months, while in Penang (HOLTTUM '40) and even in East Johore (CORNER '40) it shows a one year cycle normally, though the bare spell is not known. Probably the real vegetative period is longer than in Singapore. In contrast, the Para-rubber tree has in Singapore 13·3 months leaf-period, while it shows even in North Malaya 12 months regularly and in Ceara (4° S), Brazil, it stands two months in the resting condition. Singapore seems in this respect to be a favourable habitat for rubber production. For trees with a period of more than 13·7 months, we have no data from other districts to compare.

If one assumes that the leaf-period including the rest period* of deciduous trees is one year normally, except those with a half-year period, then this habit is maintained in those districts with distinctly dry or cold seasons irrespective of the length of the rest-period, and the periodicity in Singapore is shortened or lengthened according to the species as stated above. But in those regions with a long dry season, the vegetative period becomes far shorter than one year, so that the same trees with a short leaf-period at Singapore might display their proper length of activity, while those with a longer period might have lengthened their activity under the favourable conditions of Singapore. But if the active period of trees in Singapore be their natural length, then the length in dryer districts should be a forced one destined to become one year.

Very interesting in this respect is the fact that *Terminalia catappa,* which has a half-year period in the tropics and sheds leaves in Singapore about January to February and July or August, tends in Rio de Janeiro (23° S), according to a letter from Mr. Corner, to be of one year cycle with a long rest period in winter (May to October) when the leaves are gradually shed: it has, therefore, six months vegetative period grading into six months rest. The length of rest period seems, therefore, to be a flexible character, by adjustment of which the shifting of seasonal change is attained. Besides, there may be some trees in which the length of their activity has already become inherent at each habitat.

Trees of northern origin, as *Fagus, Carpinus, Ulmus,* etc., are provided probably with a one-year period, but those of southern origin as *Ficus, Mallotus, Albizzia,* of which some allied species

* The flowering and fruiting may occur during either the leaf-period or the resting period according to the species.

in the tropics grow continually, produce in the temperate zone their leaves until summer and close the shoot into a dormant bud in autumn. In these trees it is not clear whether the annual periodicity is inherent or induced. Leaves have their own life-time, but the shoot can continue its growth so far as the bud does not close.

§ 16. The grade of leaf-fall of trees in various districts

In Singapore, not only the leaf-fall and the length of active period, but also the grade of leaf-fall, are different from those of the other districts. Many species of trees occur on the Continent, in Malaysia and in other regions, aboriginally or by introduction. If one compares the behaviour of leaf-fall in these regions, the relative habit of trees against the dry season can be seen.

(1) Evergrowing in Singapore, but deciduous in other districts:—

Trema orientalis (Himalaya to Polynesia).

Ficus elastica (Himalaya to Java. Leaf-fall in Ceylon II–IV irregularly).

Duabanga sonneratioides (India to N. Malaya. Leaf-fall in India in IV, the hot season).

(2) Exotic trees evergrowing or evergreen in Singapore, but deciduous in original districts:—

Melia azedarach (N. India).

Antidesma bunius (Himalaya to Australia).

Sapindus mukorosii (China).

Mimusops elengi (India, Burma, Ceylon).

Tectona grandis (S.E. Asia. Leaf-fall in India XI–III, in Java VII–IX).

Tectona hamiltoniana (Burma, deciduous in hot season).

(3) In Singapore semi-deciduous, in other districts deciduous:—

Ficus religiosa (India).
Tamarindus indica (Africa to Asia).
Albizzia odoratissima (Himalaya to Siam).
Dillenia indica (India, Siam, Malaya).

(4) Deciduous in N. Malaya, evergreen in S. Malaya:—

Elateriospermum tapos (W. Malaysia).
Dillenia ovata (China, Siam, W. Malaysia).

The effect of the dry season on the leaf-fall is clearly to be seen.

§ 17. The deciduous habit and the height of crown

Most shrubs and young trees in the tropics are evergrowing, while tall trees are often deciduous. It is stated that in the highest stratum of the primary forest in the tropics many deciduous trees are to be seen (RICHARDS '52). Indeed, with the raising of the crown, not only the ascent of sap gets difficult, but also the insolation and wind are far more intense than in the lower strata, so that the lifting high over the forest canopy may induce the deciduous habit or the habit may relate with the height of crown. *Dyera* and *Irvingia* are instances of deciduous trees more than 200 feet high. But there are also tall evergreen trees of the same height, as *Balanocarpus* and *Dryobalanops*. Trees projecting higher than 100 feet are more numerous among evergrowing trees than deciduous ones in Malaya and India (CORNER '40, TROUP '21), though this may be due chiefly to the abundance of evergreen species in the tropics. Tall trees in the same family are sometimes evergreen and sometimes deciduous as shown below. (Deciduous trees and the height of trees in feet in brackets).

Juglandaceae: *Engelhardia spicata* (100), (*E. nudiflora* 100);

Moraceae: *Artocarpus elasticus* (150), (*Antiaris toxicaria* 150);

Leguminosae: *Parkia speciosa* (150), (*Koompassia excelsa* 150–260);

Anacardiaceae: *Melanorrhoea Wallichiana* (150), (*Melanorrhoea* sp. 150, *Pentaspadon* 2 spp. 150);

Sterculiaceae: *Pterospermum javanicum* (150), (*Sterculia macrophylla* 150).

It may be understood that tall trees are not all deciduous. Moreover there are many deciduous trees of relatively low height, as for instance: *Excoecaria agallocha* (30), *Cassia fistula* (30), *Sterculia rubiginosa* (30), *Flacourtia rukam* (40), *Lannea grandis* (50) and many others.

Even if the deciduous habit is fitted for the highest story of the forest, the bare period is usually short, and in wet regions or in the wet season it seems rather a waste of time for photosynthesis. If one examines the deciduous trees more closely, it becomes clear that the deciduous habit is not merely related with dryness alone. Viewed from their distribution in the tropics, the deciduous trees are not all xerophobic, on the contrary some are even hygrophobic as stated below.

§ 18. Deciduous trees and their habitats

In the temperate zone the texture of the leaves of deciduous trees and of evergreens are clearly distinguishable, namely membranous versus coriaceous, while in the tropics of uniform climate both kinds of leaf-texture are found as a generic character either in deciduous or evergreen trees, whether their habitat be wet or dry. One can not decide, therefore, from the leaf-texture alone either habit or habitat. This may be attributed to the circumstance that, under uniform climate, trees are allowed to grow continually, irrespective of their leaf-texture. On the other hand, even if the leaf is coriaceous, it tends to be deciduous, if the abscission layer is formed earlier than the new leafing, as in *Ficus caulocarpa* and others.

Most deciduous trees are mesophytic, but there are also some hygrophilous and hygrophobic trees, though the water-condition of the soil and of the air is not necessarily the same.

Hygrophilous deciduous trees indigenous to Malaya, growing in lowland forest or swampy ground are *Anisoptera megistocarpa, Beilschmiedea malaccensis, Canarium rufum, Excoecaria agallocha, Mallotus* sp., *Terminalia phellocarpa,* and *T. subspathulata.* The *Mallotus* sp. is an undergrowth tree deciduous in the swampy forest and shows that the deciduous habit can develop even in wet forest. *Excoecaria* grows in the mangrove zone. Among trees of wide distribution, some are hygrophilous and deciduous. For instance, *Cedrela toona* grows on wet soil of valleys and riversides; *Bischofia javanica* is a deciduous tree, which however tends to be evergreen in wet ground (TROUP '21). The teak-tree of monsoon regions tends to be semi-deciduous on riversides in the flood-zone (SIMON '14, COSTER '23), but in Singapore its growth is inferior and manifold (§ 8–2). Probably the shoot is hygrophobic, but the root is slightly hygrophilous. Trees which are semi-deciduous or evergrowing in S. Malaya, but deciduous in other districts, seem generally to be mesophytic or slightly xerophobic.

Among deciduous trees there are some which seem rather hygrophobic. SCHIMPER ('98, p. 262) stated that some trees shed leaves in the wet season. In Ceylon there are also about 2 per cent of deciduous trees, which shed leaves in the September rainy season (WRIGHT, '05). In Java *Spondias mangifera* sheds leaves in the wet season of January to April, and *Tetramelis nudiflora* in December (SIMON '14). In Trengganu (Malaya), an unidentified species of *Melanorrhoea* sheds its leaves in October and November at the beginning of the rainy season (CORNER, '40).

Leaf-fall occurs, not only after senescence, but also after a few days in the dark or under a wet bell-jar, in high temperature or other abnormal conditions. In the tropics the rainy season is often accompanied by damp and gloomy weather, so SIMON imagined that the leaf-fall may be attributed partly to these conditions. Naturally such a habit seems rather rare among deciduous trees in general, but there are still some that, considered from their distribution, seem to be hygrophobic. They are trees, which, in spite of their distribution widely in S.E. Asia or Malaysia or further to Australia or Africa, do not occur in Malaya or S. Malaya, as for instance:—

Ailanthus malabarica: India to N. Malaya.

Albizzia lebbec: Africa to India and Australia.

Alstonia scholaris: Ceylon to N. Malaya, Java and Philippines.

Anthocephalus cadamba: India to north of Johore, Java to New Guinea.

Butea frondosa: India to China and Java, but not in Malaya.

Dillenia aurea: India to N. Malaya and Java to Philippines.

Diospyros montana: India, Australia.

Feronia limonia: India, Siam to N. Malaya.

Flacourtia indica: India, Malaysia.

Garuga pinnata: Himalaya to Siam, Java and eastwards.

Hymenodictyon excelsum: India to N. Malaya, Java to Philippines.

Neesia altissima: Siam to Penang, West Malaysia.

Oroxylum indicum: India, China to N. Malaya, Malaysia to Philippines.

Tetrameles nudiflora: India to N. Malaya, Java to Timor.

Ailanthus flowers and fruits in Penang, but it does not thrive in S. Malaya even under cultivation (BURKILL '35). *Tetrameles* sheds its leaves in the rainy season, as mentioned above.

Roughly speaking, the deciduous habit is an internal process, in which the abscission layer is formed in a quick tempo. Its final step may be precipitated by some physiological disturbance as dryness, wetness or other condition according to the species. In a non-seasonal warm climate the habit does not matter very much, but in the temperate or monsoon regions it may have a survival value.

§ 19. The systematic occurrence of deciduous trees

Among 73 dicotyledonous families that the writer could investigate, there are naturally many families which contain no deciduous tree, such as Casuarinaceae, Elaeocarpaceae, Fagaceae, Loganiaceae, Magnoliaceae, Malvaceae, Myricaceae, Myristicaceae, Myrsinaceae, Myrtaceae, Rhamnaceae, Rhizophoraceae, Symplocaceae, Theaceae and some other small families (see Appendix), though most of the families, if they occur in temperate regions, contain deciduous trees.

Now, the deciduous trees in the tropics are distributed in various families fairly evenly, just as are the evergrowing ones. Families rich in genera and species are generally rich also in deciduous trees, though not proportionally.

Some genera contain several deciduous trees. For instance, *Artocarpus* (contains 2 deciduous species), *Ficus* (5), *Parishia* (4), *Spondias* (4), *Dillenia* (3), *Cratoxylon* (3), *Terminalia* (5), and Alstonia (6), that is, 8 genera, in 6 families. But these families contain also evergrowing species, except Guttiferae, indicating how easily the periodic habit can vary even in one and the same family.

Among the 73 families investigated, 17 Malayan families contain both evergrowing and deciduous trees, namely: Anacardiaceae, Apocynaceae, Bombacaceae, Combretaceae, Dilleniaceae, Dipterocarpaceae, Euphorbiaceae, Hamamelidaceae, Lauraceae, Leguminosae, Lythraceae, Meliaceae, Moraceae, Rubiaceae, Sapotaceae, Sterculiaceae and Ulmaceae. If one takes exotic trees into account, the following 8 families may be added: Anonaceae, Bignoniaceae, Flacourtiaceae, Guttiferae, Lecythidaceae, Rutaceae, Sapindaceae and Tiliaceae.

Of these families, the following genera contain trees of both forms of growth: *Gironniera, Ficus, Bridelia* and *Mallotus*. The genera which contain a few deciduous trees among intermittently growing ones are many (see Appendix).

Besides, there are a few tropical genera which contain among many evergreen trees only one deciduous species:—

TABLE 6

Species	NUMBER OF SPECIES		Dediduous
	In the world	In Malaya	
Beilschmiedia (malaccensis) ..	20	15	1
Dalbergia (loiveri)	120	15	1
Canarium (rufum)	100	12	1
Mallotus sp.	100	25	1
Lucuma (Maingayi)	50	8	1

These trees are therefore, so far as the Malayan species are concerned, the single deciduous species of each genus.

Moreover, even in the tropical families Anonaceae and Dipterocarpaceae, some deciduous trees are seen, and in the genus *Ilex,* most species of which are evergreen even in the temperate zone, *I. macrocarpa* in Malaya is semideciduous. There are also a few monotypic genera with deciduous species, namely: *Elateriospermum tapos* of W. Malaysia, which is in S. Malaya semideciduous, and *Feronia limonia,* which is distributed from India to the northern boundary of Malaya, is deciduous. Further in some genera of the tropics, only the single Malayan species is deciduous, though it is not known whether the other species of each genus are also deciduous or not:

Altingia excelsa: 2 spp. in the tropics.

Irvingia malayana: 4 spp.

Trigonachras acuta: 9 spp.

Tetrameles nudiflora: 4 spp.

As these cases indicate, deciduous trees occur even in a wet and warm climate, so the origin of the inherent deciduous factor seems not very complicated and can be developed in various families and genera rather optionally. The formation of the abscission layer before new leafing is its fundamental condition, and the habit can be continued so long as it is not a handicap in the struggle for existence.

§ 20. The geographical distribution of deciduous trees

In Malaya there are endemic deciduous trees, some of which spread all over Malaya, but others are confined to the northern or southern part of the peninsula. Besides, there are indigenous deciduous trees common to S.E. Asia or Malaysia. With Sumatra the affinity is the most intimate, but there are also trees common to the Philippines, New Guinea, and the Pacific Islands to Australia. On the other hand, there are also trees common to islands of the Indian Ocean and Africa, and a few show the most wide distribution over all these regions.

If most Malayan deciduous trees are the same as those of the Continent, we may assume that most of them have migrated from S.E. Asia, where a distinct dry season predominates, whereas if the trees in common are few, the relation of the deciduous habit with dryness is not essential. On the other hand, if the Malayan

elements have more in common with those of Malaysia and remoter districts, it seems more probable that at least some Malayan elements may be hygrophilous deciduous trees common to the Oceanic Islands, though even in Malaysia there are wide regions with a long dry spell. If, again, endemic deciduous trees are abundant, the habit seems to have developed of itself by mutation. Naturally such a test tells nothing about the actual course, yet it is not without interest to see the trend of the deciduous habit.

For this purpose the writer divided the deciduous trees of Malaya into three Groups: (1) those endemic to Malaya, (2) those common with the Continent, and (3) those common with the Pacific region, each with subdivisions.

	No. of species	Total
1) Endemic species of Malaya		
a: throughout the Malay Peninsula	22	32
b: the northern half	4	
c: the southern half	6	
2) Common to the Continent		
a: S.E. Asia to Philippines, New Guinea or Pacific Islands	12	49
b: S.E. Asia or Africa to Australia	7	
c: S.E. Asia to Malaysia	20	
d: S.E. Asia to Malay Peninsula	10	
3) Common to the Pacific Islands		
a: Indian Ocean to the Pacific	2	26
b: Malaysia to the Pacific	1	
c: Malaysia	3	
d: West Malaysia	20	

The number of species in these groups is in ratio of 32: 49: 26. In Malaya therefore the deciduous species common with those of the Continent are much more than the endemic ones (49: 32), but the relation with the Malaysia and Oceanic Islands is not much less, or the difference is not very significant. The groups, here classified, are however based only on a territorial distinction. But in E. Malaysia there are some islands with distinctly dry season (RENSCH '30) and Oceanic Islands have few species in common with Malaya. The most similar region, both in the climate as well as in the species in common, is W. Malaysia. If one divides all the named regions roughly into two, the wet and the dry, so the number of species of the former, including Malaya and W. Malaysia amounts to $32 + 20 = 52$, and that of the rest distributed in more or less dry regions amounts to 55, so that the both groups are nearly equal. In this respect the deciduous trees of Malaya tend in their affinities neither to the dry, nor to the wet regions.

But if a species continues its distribution after having acquired the deciduous habit, it is not enough to relate this to the present climate alone. It is necessary to consider conditions in the past. Let us examine, therefore, the past geological history of the Malay Peninsula and see whether there were some changes that might have induced the deciduous habit.

§ 21. The geological history of the Malay Peninsula

Malaya is not an ancient peninsula. It originated, together with W. Malaysia in the Cretaceous. The foundation of the Peninsula consists of conglomerate, the materials of which flowed down from the Gondwanaland and spread over both the northern and southern Hemispheres in the Mesozoic (SCRIVENOR '28). Since then, until the mid-Tertiary, the climate of the eastern Hemisphere was mild and tropical plants ranged widely from Asia to Europe. Fossil plants embedded in London clay of the Old Tertiary are common to families and genera of South China and Malaya today and even several closely related species were found (REID and CHANDLER '33). The climatic gradient from south to north of these regions was gentle and probably warm and cloudy, so that even the tropical zone was not very hot, as at present, and the temperate zone was not very cold in winter.

When the winter is not very cold, the tropical flora can flourish, as the summer is warm enough for growth. The tropical rain forest in Asia spreads at present over 28° north latitude from north-eastern Burma to the Himalayan district. At Sibsagar (27° N.), where the tropical rain-forest still predominates, the mean minimum in January is 49° F., and in the extreme attains 42° F. The rain-fall amounts to 95·5 inches (= 242·5 cm.), but chiefly in summer, while in December only 0·5 inches (= 1·3 cm.) falls, and yet there exists the rain-forest (CHAMPION '36). According to BROOKS ('22) the mild climate in the arctic regions of the Tertiary would have been attained by increasing inflow of warm surface-water from the tropics to the pole by topographical changes, even without the change of the earth's axis or continental drift.

In the Miocene Malaya made up, together with the West Malaysian Islands, the so-called Sundaland, faced eastwards to the Sahul Shelf including New Guinea and Australia, with which it was connected sometimes by a land, sometimes by a chain of archipelagoes (MERRILL '23, LAM '27, ARLDT '38). In the Pleistocene, Java separated first, then Borneo and Sumatra and lastly the Malay Islands which later were connected with the Continent.

Such a chronological sequence of W. Malaysia is shown well in the floristic affinity of its parts. So far as the Malay Peninsula is concerned, the difference of the floristic composition north and south of 77° N. makes the estimation probable (SYMINGTON '43). In the Pleistocene the Glacial Periods were repeated, and migration and changes of growth-form were also striking.

During such bewildering changes, what kind of trees gained the ability to form the resting bud is not clear. Considering the northern hemisphere as a whole, trees with the ramifying growth, as *Ginkgo,* seemed easily to endure the unfavourable season by forming resting buds. Most conifers continued their monopodial growth by forming buds in winter. *Dadoxylon indicum,* a Permian conifer of Gondwanaland in India, shows distinct growth-rings in the trunk (SEWARD '33). Also some fossil-woods with growth-rings have been found in Europe and Alaska (BROOKS '22), though most of the ancient fossil-woods show ringless wood. Naturally, even in trees with the intermittent growth, so far as the shoot-growth is manifold, the formation of growth-rings tends to be indistinct (COSTER '27, '28), so that the presence or absence of growth-rings alone can not give the evidence of intermittent growth and bud-formation.

In the era of Sundaland, the climate of Malaya was probably like present-day Burma (compare the maps in MERRILL '23 and LAM '27), where from the tropical wet forest along the western coast to the thorn-forest of the midland several transitional vegetation are seen (STAMP '25, CHAMPION '36) (§ 18). At least there would have existed some districts with a long dry spell in the Sunda-midland of that era. Therefore, if some trees originated in Sundaland, like the Dipterocarpaceae, the birth place of which is inferred to lie between Borneo and Malaya (SYMINGTON l.c.), they may have acquired the deciduous habit in spite of the tropical origin. In this respect, the comparative study of resting buds and growth behaviour in general of tropical trees may tell us the previous history of their ancestors.

But, since the formation of the Malay Peninsula, there have elapsed ten thousand years or more, and, considered from the viewpoint of adaptation, it seems rather strange to have perpetuated for so long a time the deciduous habit in a uniform climate. Perhaps among the genetic characters some are easily formed but not easily reversed, while others behave inversely, though we do not know how the deciduous and bud-forming characters are realized as internal processes. The transformation of the bud-forming

character within a certain systematic group in respect to the range of distribution tells us however something about the evolutionary change of the growth habit of trees indirectly (§ 24).

§ 22. The transition of shoot-growth from the evergrowing to the deciduous

The growth process, whether periodic or not, is essentially an inherent character. Even if it is automatic, it is realized only when the external conditions allow, while under abnormal conditions it can be realized only with difficulty. On the other hand, the paratonic reaction goes on subject to environmental change, sometimes freely and sometimes enforced by it, so that the reaction proceeds either actively or passively, and varies widely in its behaviour. Or, in other words, the internal and external factors work together intricately.

Trees of ancient types show mostly non-periodical gradual growth. Perhaps the ancestors of all phyla of trees were non-periodic in their growth and so far as they remain in wet and warm regions, they have continued their habit unaltered, as for instance, tree-ferns, cycads and palms with single thick stem, in which substituting growth is not generally permitted. Most conifers show the monopodial growth as much as possible, even if provided with the means of substitution. In dicotyledonous trees, the mode of branching is represented in various ways. The tropical trees of primitive families show mostly monopodial growth, but even in trees of advanced families, so far as they grow in a favourable environment, monopodial growth still predominates, while in the temperate zone sympodially ramifying trees are usual, especially those with slender twigs. This is partly due to the dying out of the apical parts through physiological dryness, as may be estimated by the number of wilting buds, which are more abundant after a severe winter. But in some trees terminal buds die in summer as an inherent character, as in *Tilia, Ulmus, Syringa* and others. In either case the more easily the substitution occurs, the more adaptable is the tree to severe and variable conditions.

But, even in Singapore, there are a few trees in which the terminal bud dies out (§ 9) as *Xanthophyllum Curtisii* and *Crataeva Roxburghii*. The resting buds of the former (Fig. 1), both terminal and axillary, are peculiar in construction. They are protected by a pair of prophylls ca. 0·5–1·5 cm. long, forming an acute quadrangular white pyramid, very conspicuous amidst the dark green leaves. The inside of the scales consists chiefly of an air chamber with a tiny bud at the base. What teleological meaning

such a construction has is not clear, but absorption and conduction of heat of insolation will be relieved at least for a while. In spite of such a structure, the terminal bud dies away early every season as an inherent process. The ancestor of the species seems therefore to have been well adapted to dry spells, though in Malaya, especially in Singapore at present, no such crisis may happen.

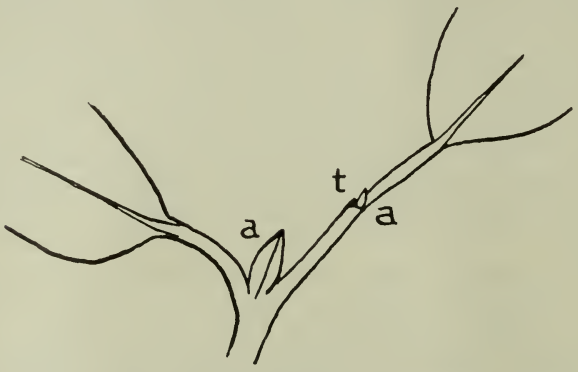

Fig. 1. Xanthophyllum Curtisii.
t, terminal bud withered; a, axillary buds.

On the other hand, among some families and genera of the intermittently growing habit, one can find a few species of the evergrowing habit in Singapore. For instance, *Gironniera subaequalis, Elaeocarpus sphaericus, E. stipularis, Campnosperma auriculata, C. minor, Adinandra dumosa, Archytaea Vahlii,* and *Symplocos fasciculata.* Perhaps there may be still more. As most trees of these families and genera are distributed on the Asiatic Continent and are intermittent or deciduous in their growth, so these evergrowing species seem to have acquired the habit in Malaya.

In temperate regions, all trees, whether evergreen or deciduous, are intermittent in their growth, forming the resting buds and shedding leaves in a definite season. But when they are transplanted to warmer regions, their behaviour differs specifically. For instance, the beech-tree transplanted to southern regions sheds leaves though with delay, ultimately, subject to the autonomic periodicity, while fig and mulberry-trees transplanted to the tropics grow continually, becoming positive in activity on account of the favourable conditions.

Conversely, trees of southern origin as *Robinia, Sterculia* and others, do not close the shoot in the temperate regions, but form new leaves continually and indefinitely until the arrival of the cool season, when the bud-forming process is at length induced. The

palms in the temperate zone, for instance *Trachycarpus excelsa* of Japan, show intermittent growth, flowering in late spring by sending out 5–7 inflorescences at once from the axils. The morphological sequence is just the same as in tropical palms with axillary inflorescences, which appear however in the tropics after development of successive leaves with equal intervals, one by one, non-seasonally. The flowering of palms in the temperate regions is, therefore, externally controlled intermittent growth, though it is not known whether this periodic flowering has become inherent or is still reversible in warmer regions.

There are besides a few widely distributed trees which are ever-growing in Singapore, but deciduous under seasonal climate, as *Trema orientalis,* distributed from India to Polynesia. We can not say which of the two regions is the normal and which is the phenocopy (GOLDSCHMIDT '35), or whether each represents an ecotype (TURESSON '30).

Physiological reactions are controlled naturally by prevailing conditions, but so far as a species shows a local difference in its activity, even if of slight character, it is not easily modified by mere transplantation to other localities. In the temperate regions the same species of tree from the north is generally earlier in leafing as well as in leaf-fall than that from the south; the former is more frost-resistant than the latter. The variation is fixed as an autonomic character. As a rare case, it was found, however, in *Carya* of temperate America, that a southern species was more frost-resistant than a northern species (WHITE '35); it indicates the existence of a genetic character not apparent in the original southern district. TURESSON ('30) has found in ca. 30 perennial plants distributed widely in Europe and Asia, north and south as well as inland and coastal, that the species in each locality forms an ecospecies in flowering, height of stem and so forth, adapted to the local environment. Even in the photoperiodic response, FÜRTAUER ('40) found in *Epilobium hirsutum,* which spreads from Abo (61° N.), Finland to Kirstenbosch (34° S.), S. Africa, that the photoperiodic response is long day in the high latitude, short day in the low latitude and neutral in intermediate regions, representing hereditary local races.

Similarly the periodicity of the tree-growth in each locality seems mainly of inherent character (see also § 25). Recently the behaviour of polygenes in various quantitative characters has been taken up in the experimental field and analyzed in detail (see for instance: MATHER et al '43, WOODWORTH et al '52). The local difference of the periodic behaviour of trees seems in this respect to be an instructive theme for further study.

§ 23. The morphological development of the resting bud with special reference to the formation of scales

For the formation of the resting bud three procedures are involved: (1) the growth in length is retarded by the development of a rhythmic tendency, (2) the leaf-primordia formed on the growing point cease to grow further till to the next season, and (3) some primordia metamorphose into the protecting members, though in the tropics these processes are gradually simplified.

In primitive tropical families, as Anonaceae and Myristicaceae, most of the trees are evergrowing without closing the shoot. The formation of buds is in this respect a change of growth reaction for protection of the growing point against unfavourable conditions. But the restriction of the shoot growth does not necessarily cause the formation of bud-scales. The latter is an independent process, and trees destitute of that ability, when restricted in their growth by drought, can not form a resting bud, e.g. *Carica, Acalypha, Jatropha, Hibiscus, Lantana* and others (COSTER '23).

In tropical trees with intermittent growth, the terminal portion of the resting shoot is usually not covered by scales, but loosely by a few young leaves, provided often with dense hairs or gum-resin. Morphologically, these procedures are far simpler than the metamorphosis of foliar organs.

But some deciduous trees, the genera of which are of continental origin, as *Kurrimia* and *Pygeum,* are provided with well-formed scales, and those from central and tropical America, as *Achras* and *Couroupita,* with metamorphosed succulent petioles. Even in evergreen species of *Quercus* and *Castanopsis,* which originated in calid regions, the buds are covered with dense corky scales, like those of the temperate species. The same holds true with trees transplanted from the calid regions such as *Eryobotrya, Cinnamomum,* and *Pittosporum.* Scaly leaves are here not only the reduced phyllome, but with suberification added.

In trees of Magnoliaceae, Moraceae, and Rubiaceae, in which the terminal bud is protected, as a family character, by a pair of stipules or petiolar bases, the growing shoot can become a resting bud without special morphological contrivance so that the trees of these families are found in various growth-forms from the evergrowing to the intermittent or even to the deciduous, and distribute themselves widely in calid regions.

The development of foliage leaves of intermittently growing shoots is sometimes gradual with transition from scales or protective leaves to normal ones in each season, but usually the change is as abrupt as in temperate trees of the northern origin, in which even a definite number of foliage leaves is laid down in the bud

(LUBBOCK '99). For instance in *Fagus, Carpinus,* etc., after development of new shoots during one month or so, the twig terminates with apical and axillary buds of the next spring without growing further, notwithstanding that the season is just getting warmer. Bud-formation here is, therefore, not induced by low temperature, but only by an inherent process.

In *Carya* of N. America, at first about seven scales are found during spring and early summer as the covering of the bud for the next spring; 3–4 pairs of foliage leaves follow during the summer and, then, 2–3 heteromorphic scales, which represent the outermost scales of two years later and shed themselves soon after the growth of the inner bud (FOSTER '31). Similar development of foliar organs is seen also in *Aesculus* (FOSTER '29). In *Pinus sylvestris,* a tiny bud of two years hence is already formed on the tip of the bud of the next year (LUBBOCK, l.c.), and in *Salix reticulata* of the arctic region, the new shoot is formed two years and a half in advance, in accordance with the short vegetative season (RESVOLL '25). Even in *Shorea Hemsleyana* of Dipterocarpaceae, on the top of each bud is formed a young tiny bud of two seasons later (Fig. 2).

The tree is endemic to S. Malaya and Sumatra and ecologically has no need to form such a young bud with hurried tempo. At

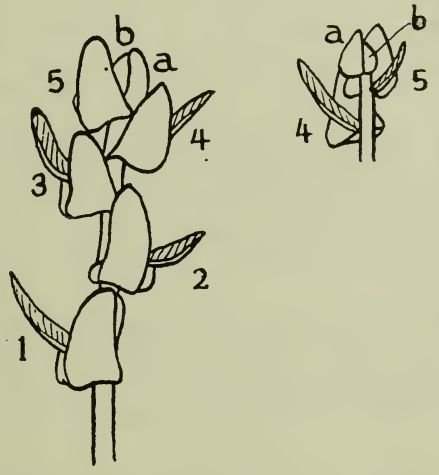

Fig. 2. Shorea Hemsleyana × ca 4/5. Right figure seen from the opposite side.

A bud just elongating, with leaves 1–5, and with young bud of next season on the top covered by stipules a and b. (Compare SYMINGTON '43, p. 71) (ca. 4/5).

any rate, such a process is hardly conceivable without the assumption of a specific hormonal activity.

All these cases show that the formation of buds is not a direct reaction to unfavourable climatic change. On the contrary, it occurs as an inner process rhythmically after development of foliage leaves, either in warmer or in colder regions, and even in the case where low temperature or drought induce bud-formation, it is only an indirect condition and not able to cause bud-formation by itself, unless the plant is endowed with bud-forming ability genetically.

If we summarise the development of the resting bud from the ever-growing to the deciduous, it may be written as follows:—

(1) Evergrowing bud.

(2) Periodic fluctuation of leaf-size on the shoot.

(3) Change of proximal leaves of each period to protecting leaves, small in size, often more hairy or producing anthocyan, etc. and falling early.

(4) Protecting leaves reduced to scales, often represented by petioles or stipules, embracing or surrounding the young shoot tightly and often corky.

(5) Young bud ceases to grow after forming a definite number of foliar organs.

(6) Young bud hastens further to form still younger bud of two seasons later.

Each species of trees has its own rank of bud-development, as mentioned above.

In the evergrowing shoot leaf-fall keeps pace with the opening of new leaves, one after another. After acquiring the periodic tendency, however, the basal leaves fall early, while the laminar leaves remain longer as assimilating organs and the more the periodic tendency is intensified, the more simultaneous become leafing or leaf-fall.

In conclusion, the formation of the bud is realized by the intricate co-operation of the hereditary characters and the environment. In the tropics the formation of buds is often autonomic, while in the temperate zone the seasonal change may induce it.

AXILLARY BUDS: Now, concerning the axillary buds, they are in some shoots just bare like the terminal one, as in *Alangium Ridleyi, Adenanthera pavonia, Delonix regia* and many species of Anonaceae and Myristicaceae. In *Spathodea campanulata* the prophylls are also green, though different in shape. But in most

cases they are protected by a pair of prophylls, rather tightly even in evergrowing shoots. In the evergrowing *Averrhoa* and *Caesalpinia sappan,* although the terminal bud is bare, the axillary buds are protected by prophylls, and in *Sterculia ferruginea* they are covered with many scaly stipules besides the prophylls. Naturally most of the axillary buds remain dormant without further growth, except when they develop as cauline inflorescences after a long spell.

It may be seen, therefore, that in the wet tropics the grade of protection of axillary buds is manifold and not intimately related with the mode of the shoot-growth.

§ 24. The retrogression of the bud-forming ability

Bud-forming ability does not always proceed unidirectionally to the complication of scale-members. As already stated (§ 22), some tropical trees, viewed from the systematic and comparative standpoints, seem to be transformed from the intermittent to the evergrowing, together with retardation of the bud-forming ability. For instance the genus *Adinandra,* which is distributed mainly in mountainous regions of S.E. Asia to Malaysia, produces well-protected buds, whereas *Adinandra dumosa* spreads over the lowland of W. Malaysia growing continually, forming no resting bud. *Gordonia* of the same family spreads over the highlands of tropical regions widely, while *G. singaporeana* grows in the lowlands of Malaya, and, though the growth is slightly intermittent (§ 10), never forms a resting bud, and suggests equally the transition to the evergrowing. The genus *Alangium,* distributed from Africa to the Pacific Islands and Formosa, seems distinctly intermittent in its growth, but *A. Ridleyi,* an endemic species of Malaya, has no scales in the resting bud, which is covered only by two young leaves as if nearly evergrowing. *Peltophorum pterocarpum* is deciduous with leaf-fall twice every year, well adapted to the monsoon-regions ranging from Indo-China to Malaya and further to Australia; in Singapore, however, it does not close the bud, which is covered only by a few basal leaves densely clad with hairs. There may be many more cases of such a retrogression of bud-formation.

Thus bud-formation goes on, either in evergreen or deciduous twigs, not always parallel with the cessation of shoot-growth. Under a favourable climate, the bud can be much simplified. The formation of bud-scales is therefore a different process that may or may not accompany the retardation of shoot growth. But, as one

looks at trees as a whole, including those of the temperate zone, the two processes are seen to be correlated with each other, and the more tightly the bud is closed, the more intermittent is its mode of growth. Though originally different, these two processes are combined together by natural selection, except under uniformly favourable conditions. The internal processes of bud-formation are not clear, but hormonal activities derived from inherent characters undoubtedly control this behaviour. Periodicity of tree-growth as a whole is, indeed, sufficiently comprehensible only when one assumes hormonal activity as an inherent process.

§ 25. The intermediation of hormonal activity on the process of periodicity

As stated above, the formation of scales, foliar leaves, etc. in a definite order around the growing point of trees rhythmically is not caused by the direct effect of climatic changes, but as a consequence of internal specific processes that ought to be attributed to the quantity and distribution of respective hormones. An interesting example of abnormal scale formation caused evidently by the disturbance of hormonal distribution, was observed by the writer in a growing shoot of *Lucuma Maingayi* (Fig. 3).

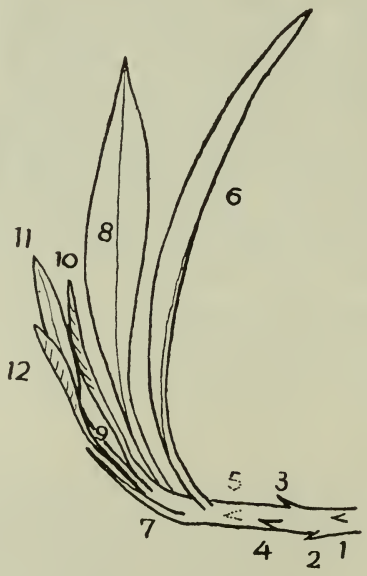

Fig. 3. A young shoot of *Lucuma Maingayi* grown horizontally.

In a new shoot with scales and foliage leaves in 2/5 phyllotaxis, the 1st to 5th phyllomes were scales and the 6th, 8th and 10th were foliage leaves, while the 7th and 9th between the above mentioned leaves should have been foliage leaves but were typical scales. The new shoot was in horizontal position and the reverted scales were on the underside. It is therefore conceivable that some hormones, destined for green leaves or an antihormone to such, received disturbance on both sides, upper and lower, at the beginning of differentiation, and as a result the disorder ensued, just like the behaviour of auxine in geotropic response (SCHRANK '50). This fact shows that the final form of the leaf is not predistined by the primordium. It may also be inferred that in *Kurrimia* and others mentioned previously (§ 23), at the beginning of formation of the resting bud, some hormones appear that prevent the normal development of foliage leaves, and after exhaustion of the same, the primordia tend to be normal. But in *Carya* (FOSTER, l.c.) the leaf-forming hormone seems to be exhausted after the appearance of a definite number of leaves, and then an inversed course of hormonal activity takes place forming the scales again.

The shoot of *Bridelia* shows the first indication of the rhythmic growth of leaf-size, as already mentioned (§ 10). If the leaf-size is determined absolutely by the quantity of nutrient materials, it seems more probable that the basal or apical portion of the shoot in each season would produce the larger leaves. In most tropical trees with intermittent growth, the leaves at about one-third from the base of the new shoot tend to be the largest, but in *Cassia* and others the leaf-size increases in the terminal direction. In other words, there is no rule concerning the distribution of leaf-size in shoots of each season. Similarly in temperate regions it is manifold according to species (DENNERT '26). As the leaf-primordia around the growing point are uniform in size, so the subsequent difference in size should result from the mode of cell-division induced by the activity of the respective hormones, while each cell attracts its own nutritive materials from below.

In the shoot of each season, the internodes belonging to the scales and incomplete leaves are generally very short, but in some species they grow much longer than those of the foliar leaves, for instance in *Actinodaphne malaccensis, Phoebe macrophylla, Knema laurina, Diospyros lanceifolia, Ptycopyxis costata* and the basal portion of apposed twigs of the Terminalia-type. It is clear therefore, that there is no causal connection between leaf-size and length of internode, even if in most cases they are more or less

proportional. Were they to be connected, it might be attributed to nutrition, but, as it is not really so, it ought to be attributed at least to two groups of hormones, which effect the leaf-size and the length of the internode respectively. They can behave independently according to species.

Now, concerning the leaf-fall, it is well known that this is affected by the formation of the abscission layer and the separation of cells along it. The layer is formed generally at the base of the petiole, for the formation of which some hormonal activity should be concerned.

For instance, the tomato does not form the abscission layer on the leaf, but the fruit is provided with a junction, from which it separates at maturity. But there was found a mutant which failed to form the junction, so that the ripe fruit was detached from the receptacle (BUTLER '36). This shows that a genetic factor controls the hormonal activity. The abscission layer is not formed, however, always in a definite position. The leaf-cutting of the sweet potato sometimes forms the abscission layer abnormally in the middle of petiole (YASUI '46). This fact indicates that, during the formation of the layer, some substance, probably a precursor of a hormone of cell division, descends from the lamina through the parenchyma downwards and meets on the way with an ascending substance from the petiole and is activated by it. That the abscission layer has a smooth surface, may be attributed to the flatness of the diffusion front, even though it is often curved according to species (PFEIFFER '28).

The formation of an abscission layer is relatively rare in tree-ferns, monocotyledonous trees, and herbs. Even in conifers some do not form it, as *Cunninghamia, Araucaria, Cryptomeria,* while *Taxodium, Metasequoia,* etc. form it at the short-base, just like *Canangium odoratum, Sonneratia acida,* and *Populus nigra.* In dicotyledonous trees, whether evergreen or deciduous, and whether in the tropics or in the temperate region, this process goes on regularly. Especially in the temperate region it occurs not only before the new leafing, but also before the severe winter, well understood as the adaptation. In trees of one and the same species, a delicate difference of various characters is often found, especially in cultivated forms. For example, in Para-rubber trees grown in the same plantation, some shed the leaves earlier, but some later, and this is characteristic of each clone. As to the quality and yield of the latex a similar difference is seen (SCHWEIZER '32). In avenue trees of *Aesculus, Fagus,* and *Ulmus* there are seen also a

difference of leafing and leaf-fall according to trees, which show the same difference every year (LUBBOCK l.c., WELLENSIEK '34). This is also seen in *Ginkgo*-trees, the so-called living fossil. Whether these characters may be transmitted through seeds or not wants experimental proof, but at all events the last step of the physiological process is realized by the activity of cells induced by hormones, by which the kind of materials, the amount and time of secretion, their co-operation or antagonism, etc. are determined inherently, even if their actions are affected at the same time by external conditions.

In herbs, there are many cases in which the seasonal behaviour has been genetically investigated. For instance in *Hyoscyamus niger,* there are annual and perennial races, but the habit can be altered by low temperature or by grafting (MELCHERS '39). Concerning the periodicity of the nyctinastic movement of *Phaseolus multiflorus,* there was found an inherent variation of 15–35 hours at 22° C. according to individuals, and the statistical mode for one cycle was 25 hours (BÜNNING '33). Yet under natural conditions their proper cycle is controlled to 24 hours. Moreover, there is a difference of the cyclic course of movement. In some individuals the leaves sink quickly and lift slowly, while others behave in the inverse way (BÜNNING '36).

The effect of synthetic hormones on the flower-formation and the ripening or abscission of fruits is well known. The fruiting of papaya-trees is noteworthy in this respect. Axillary female flowers open successively and continually, but the further development of them ceases after 10–20 fruits are formed, though all flowers are evenly pollinated, and after a few months the next crop begins forming a second group of fruits, and so on; it seems nothing but a hormonal control.

In Singapore there are some trees which do not flower or bear fruit, as for instance *Ravenala madagascariensis,* which flowers and fruits in Burma. *Borassus flabellifera, Nephelium litchi,* and *Bouea macrophylla* can ripen in Penang. It is said that the sterility may be attributed to the wet climate. But it is not clear, whether a wet climate alone is responsible, or whether intense insolation or a definite thermoperiod (WENT '48, '49) or photoperiod is needed. After all, it ought to be related with the production of the hormone-complex.

In effect, the periodicity of tree-growth is controlled by various hormonal activities as well as by the environment. Some hormones are formed as an inherent character almost invariably, but others

are more or less controlled by the external conditions. The hormones that partake in bud-formation and other autonomic processes are formed nearly independently of seasonal conditions, especially under the uniformly favourable climate. The formation of hormone in the case of leaf-fall or of abscission layer becomes the more intense, the more susceptible the tree is or the more severe the climatic changes. Conversely, the more favourable the conditions or the more insensitive the tree, the more autonomic is the production of hormones.

§ 26. Conclusion

If we compare trees in tropical and temperate regions, each group shows many adaptive characters. In the tropics there are many monopodial trees of primitive type, while in the temperate regions most trees, except some conifers, are ramiferous with slender twigs provided with numerous growing points in the form of axillary buds, which are able to substitute injured parts. Regeneration is easier in conifers than tree-ferns, and in dicotyledonous trees than monocotyledonous ones, as may be seen from the fact that monocaulous thick-stemmed trees scarcely extend further north than the calid region.

The existence of deciduous trees in the tropics of uniform climate is, however, not adaptive in its nature. The habit is not directly concerned with water or temperature relations. It is an inherent character in its origin, just like the evergrowing and intermittent growth-habit.

In the temperate region, from the systematic point of view, most deciduous trees are of northern origin, but in the tropics the deciduous trees are distributed in various families fairly evenly, being generally more abundant in larger families. There are various genera which contain both evergrowing and deciduous species, and even in some genera of tropical origin one can find a few deciduous species. The periodic habit of trees seems, therefore, to arise in any region in any family, so long as certain changes of hormonal activity can occur.

Geographically, the deciduous species of Malaya are related with those of both Continental Asia and Malaysia, though the former has slightly more species in common than the latter. If one divides all the related regions roughly into two, the wet W. Malaysia and other drier districts, so the number of deciduous species is also nearly the same. Thus the deciduous habit has no preference for the dry or wet habitat.

Considered from the geological conditions in the past, Malaya constituted in the early Pleistocene the western part of the Asiatic continent, the so-called Sundaland, and there might have been many chances for origination of deciduous trees in the midland of that era, which were distributed then to the coastal region, now representing the Malay peninsula, where they have retained their habit unaltered. But there are, on the other hand, some genera, most species of which are intermittently evergreen, that occur on the mountain region inland with some species distributed in the lowland with evergrowing habit. Growth-habit seems, therefore, not generally changeable, yet possibly so in some genera.

Periodicity of tree-growth is the rhythmical advance of the growth-process realized by various consecutive reactions. Partial aspects of it, like leafing, leaf-period, leaf-fall, etc. show sometimes even clonal variations with respect to the calendar date, which occur fairly precisely according to stocks. Such trivial characters have originated internally and are transmitted to the offspring. It has been called the *stockwise* variation in this paper.

The real process is not known, but, so far as it appears as an external character, it stands in direct bearing with the environment, and the more favourable the condition of the district, the more freely the inherent ability exhibits itself; conversely, the more unfavourable the local condition, the more restricted is the playground of expression, whether autonomic or paratonic. And the more restricted the existing conditions, the more adaptive seems the character to one's eye, and the more favourable the condition, the more untidy becomes the habit.

After all, the periodic habit, or the change of it, is not necessarily the adaptive, but, so far as the environment permits the habit, the tree can exist competently mingled with trees of other habit. That in Singapore such various growth-habits are displayed may be attributed to these circumstances.

§ 27. Summary

(1) In the tropics of uniform climate, as at Singapore, there are in tree-growth various transitions from the evergrowing to the deciduous, so that it is not enough to classify the trees simply as evergreen and deciduous as in temperate regions.

(2) Periodicity of tree-growth is characterized by the activity of the growing point as well as by the mode of branching. The former includes the continuous, the intermittent and the manifold growth, and the latter the terminal and the lateral branching. By

combination of these two categories, one can distinguish six types of tree-growth morpho-physiologically. They may be classified further in detail.

(3) Evergrowing trees are everleafing with the growing bud at the apex of the twig, and the leaf-size and the length of internode are uniform.

(4) Leafing of intermittently growing trees is seasonal, contemporary or non-seasonal, and at the end of each period a resting bud forms on the shoot-apex. Leaf-size and the length of internode are variable, usually with a sudden change in appearance of the cork-layer between each period.

(5) Manifoldly growing trees show a branchwise difference in the developmental phase caused (*a*) by dying out of the terminal bud or the apical portion of the twig or by forming the inflorescence; (*b*) by trees growing to a fairly big size; and (*c*) by the exotic nature of trees with intermittant growth, their branches having a strong inherent tendency to rhythmical growth, which is shifted, however, according to individual branches under the uniform climate.

(6) The deciduous trees are rather conspicuous in their appearance, but they represent only a special case of intermittent growth, the distinction being only whether leaf-shedding proceeds or lags behind the leafing, whence arise all sorts of transitions.

(7) The leaf-period of deciduous trees in Singapore varies from three months to more than two years according to species, usually with a short bare spell, but this has nothing to do with the hibernation of temperate trees. The frequency of seasonal leaf-fall is 1–3 times per annum according to species, that of the contemporary ones 3–4 times, and among the non-seasonal ones some are shorter and others are longer than one year.

(8) Four categories of flowering can be distinguished, as in the case of leafing. Everflowering is limited to a certain number of evergrowing trees, while the rest are seasonal, contemporary or non-seasonal, just as in the intermittent and manifoldly growing trees. Ever- and non-seasonal flowerings are autonomic in nature, while seasonal and contemporary flowerings are chiefly determined by trifling changes of the weather.

(9) In Malaya, evergrowing trees together with the manifold ones compose at most about one-fifth of the total indigenous tree-species, and the deciduous about one-twentieth, the rest being the intermittent evergreen trees.

(10) Deciduous species occur there fairly evenly in various dicotyledonous families. Most of these families include not only the usual evergreen trees with periodical growth, but also evergrowing as well as deciduous ones, indicating that the deciduous habit may occur in various families rather optionally.

(11) Some trees, though deciduous in other regions as India and Malaysia, may be evergreen in Singapore, while others are not seasonal in their leaf-shedding.

(12) In the Malay Peninsula there are, besides endemic deciduous trees, those common with Continental Asia or the Oceanic Islands—chiefly W. Malaysia—or those distributed in both regions, so the deciduous trees as a whole show no preference as to the habitat, whether dry or wet.

(13) There is also no intimate relation between the deciduous habit and the height of crown, tall evergreen trees being more abundant than deciduous ones. Low deciduous trees are also met with not infrequently.

(14) Deciduous trees are, moreover, not all the same in water relations. There are, besides many mesophytic trees, some hygrophilous and others hygrophobic, the former growing in wet swampy forest and yet deciduous, while the latter do not occur in S. Malaya.

(15) The Malay Peninsula, as a land on the Sunda Shelf, was during the Tertiary period a part of the Asiatic Continent together with W. Malaysia, so that under the then predominating climate there might have originated a number of deciduous species in the midland of that area, which retained the same habit unaltered, while others seem to have changed their habit from the periodic to the evergrowing after the formation of the present peninsula since the Pleistocene.

(16) Generally, intermittent growth, whether evergreen or deciduous, is accompanied by the formation of a resting bud. But these two processes are not always carried on in the same degree. Under a favourable climate the latter is more easily simplified than the former.

(17) The formation of leaf-scales may be attributed to hormonal activities. Similarly the formation of the abscission layer, the length of periodic activity and many other characteristics of trees are all controlled internally and show even clonal differences. This is especially evident in the uniform climate like that of Singapore, where various growth-habits are displayed without restriction, whereas in the temperate or monsoon regions the external control predominates.

Appendix

The periodicity of tree-growth in four types, together with localities. Exotic genera and species in parenthesis.

Abbreviations

Periodicity types: e: evergrowing, m: manifold, i: intermittent, d: deciduous.

Localities

Ad: Andaman Islands
Af: Africa
Am: America
As: Asia
Ass: Assam
Au: Australia
B: Borneo
Br: Brazil
Bu: Burma
CAm: Central America
Cd: Calid Regions
Ce: Celebes
Ch: China
Cosm: Cosmopolitan
Cy: Ceylon
EAs: Eastern Asia
EMs: East Malaysia
Eu: Europe
F: Formosa
Hm: Himalaya
Hond: Honduras
I: India
IC: Indo-China
IO: Indian Ocean
J: Java
Jam: Jamaica
Jp: Japan
M: Malaya
Mc: Mascarene Islands
Med: Mediterranean
Mg: Madagascar
Mo: Molucca
Ms: Malaysia
Mx: Mexico
NAu: North Australia
NB: North Borneo
NC: New Caledonia
NEM: North-East Malaya
NG: New Guinea
Nic: Nicobar Islands
NM: North Malaya
NT: North Temperate
P: Pacific Islands
Per: Peru
Ph: Philippine Islands
Po: Polynesia
Q: Queensland
S: Sumatra
SAf: South Africa
SCh: South China
SEA: South-East Asia
Si: Siam
SM: South Malaya
Sol: Solomon Islands
T: Tenasserim
Ti: Timor
Tr: Tropics
TrAf: Tropical Africa
TrAm: Tropical America
TrAs: Tropical Asia
TrM: Tropical mountains
Ven: Venezuela
WI: West Indies
WMA: West Malayan Archipelago
WMs: West Malaysia
WP: Western Pacific Islands

Genera	Distribution	No. of species	Do of Malaya	Species	Localities	e	m	i	d
				Alangiaceae					
Alangium	Am-P	22	7	Ridleyi	m			i	
				Anacardiaceae					
(Anacardium)	Am	8		(occidentale)	SAm			i	
Bouea	I-Mo	5	2	microphylla	WMs			i	
Campnosperma	As,Af,Am	10	3	auriculata	WMs	e			
,,				macrophylla	WMs			i	
,,				minor	M	e			
Dracontomelum	I, Ms, P	5	1	mangiferum	NM				d
(Lannea)	Af, I	12		(grandis)	I				d
Mangifera	SEA-Ms	40	20	caesia	WMs			i	
,,				foetida	WMs			i	
,,				(indica)	I		m		
Melanorrhoea	WMs	15	10	malayana	NM				d
Parishia	Bu, Ad, WMs, Ph	10	5	insignis	Ad, M				d
,,				Maingayi	M				d
,,				paucijuga	M				d
,,				pubescens	M				d
Pentaspadon	T, M, B	few	3	officinale	M				d
(Pistacea)	Med, As, Mx	5		(formosana)	F		m		
(Pleiogynium)	Q	1		(Solandrii)	Q		m		
Semecarpus	TrAs, Au, Po	40	10	vernicifera	F		m		
Sorindaea	Af, Mg	20		madagascariensis	Mg		m		
(Spondias)	TrAs, TrAm	6		(cytherea)	P				d
,,				(lutea)	Am				d
,,				(monbin)	Am				d
,,				(pinnata)	I-Mo				d
				Anonaceae					
Anaxagorea	Am, As	8	2	javanica	Si, M, B, S			i	
(Anona)	Am,Af,As	60		reticulata	WI				d
Canangium	Bu-Au	2	2	odoratum	Bu-Q	e			
Drepananthus	S-NG, Ph	8	4	pruniferus	M	e			
,,				ramiflorus	M, S	e			
Polyalthia	As, Af, Au	60	40	Beccarii	M, B, S	e			
,,				stenopetala	M	e			
Xylopia	Tr	100	16	ferruginea	M, S, B			i	
				Apocynaceae					
Alstonia	Af, As, Au, Po	30	6	angustifolia	S, M, B				d
,,				angustiloba	M				d
,,				latifolia	M, B				d
,,				macrophylla	NM, B, Ph, NG				d
,,				scholaris	I, Cy, Ms, Au				d
,,				spatulata	WMs				d
Cerbera	I-WP	5	2	manghas	Ms	e			
,,				odollam	I, M, S	e			
Dyera	M, S, B	2–3	1	costulata	M				d
Ervatamia	Tr	170	10	corymbosa	M	e			
,,				dichotoma	I, Cy	e			
Kopsia	SEA	12	7	fruticosa	Bu	e			
,,				singapurensis	M	e			
Ochrosia	Mc,As,Po	12	7	oppositaefolia	Mc, As	e			
(Plumeria)	Am	3		(acuminata)	Mx		m		
,,				(obtusa)	Am	e			
(Thevetia)	Am	10		(peruviana)	Am	e			

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
Aquifoliaceae									
Ilex	Cd	200	2	cymosa	WMs			i	
,,				macrophylla	WMs				d
Asclepiadaceae									
(Calotropis)	Af, As	3	1	(gigantea)	I	e			
Araliaceae									
Arthrophyllum	Ad-NG	10	8	diversifolium	WMs	e			
(Brassaia)	Au	1		(actinophylla)	Au			i	
Schefflera	ETr	80	30	heterophylla	M, S			i	
Bignoniaceae									
(Catalpa)	Am, EAs	10		(longissima)	WI		m		
(Jaccaranda)	SAm	30		(filicifolia)	SAm			i	
(Kigelia)	Af, Mg	3		(pinnata)	Af				d
Oroxylum	I, NM, C, Ph	1	1	indicum	I-Ph, NM		m		
(Spathodea)	Af	2		(campanulata)	Af	e			
(Stenolobium)	Mx-SAm	4		(stans)	SAm	e			
(Stereospermum)	ETr	20		fimbriatum	Bu-NM				d
(Tabebuia)	Cd			(rosea)	Mx			i	
,,				(triphylla)	WI		m		
Bixaceae									
(Bixa)	Am	1		(orellana)	Am	e			
(Cochlospermum)	Tr	12		(religiosum)	I				d
Bombacaceae									
(Adansonia)	ETr	10		(digitata)	Af				d
(Ceiba)	TrAm	10		(pentandra)	Tr				d
Durio	As	12	6	zibethinus	Ms			i	
Neesia	WMs	6	3	altissima	M, B, S, J				
(Ochroma)	SAm, WI	1		lagopus	Br	e			
(Pachira)	Am	4		(aquatica)	Am			i	
,,				(cyathophora)	Am			i	
Salmalia	Af, As, Au	11	2	malabarica	Hm, Cy, Bu, Ms, Au				d
,,				Valetoni	Ms				d
Borraginaceae									
Cordia	Tr	300	4	dichotoma	SEA, Ms, Au, Po			i	
,,				(sebastina)	TrAM, WI			i	
,,				subcordata	I-WP		m		
,,				(umbraculaeformis)	TrAm			i	
Burseraceae									
Canarium	Af, I, Ms, Po	109	12	(album)	IC			i	
,,				nitidum	M			i	
,,				rufum	M				d
Santiria	Ms	30	15	laxa	M			i	
,,				(rostrata)	B			i	
,,				rubiginosa	Bu, IC, M, S, J				d
,,				tomentosa					d

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
Cactaceae									
(Cereus)	Am	300		(hexagonus)	Am	e			
(Peireskia)	Tr, Am, WI	19		(grandifolia)	Am			i	
Capparidaceae									
Crataeva	Tr	20	2	religiosa	ETr		m		
,,				(Roxburghii)	I, Cy, IC, Si		m		
Caricaceae									
(Carica)	Am, Af	21		(papaya)	Am	e			
Casuarinaceae									
Casuarina	Au, Ms, I	23	1	equisetifolia	I-P	e			
,,				(sumatrana)	Bu, WMA	e			
Celastraceae									
Elaeodendron	Cd	30	1	(quadrangulatum)	Br	e			
Kurrimia	I, Ms	3–4	2	paniculata	I, WMs		m		
,,				robusta	I, WMs			i	
Combretaceae									
Lumnitzera	IO-WP	2	2	coccinea	Af-P	e			
,,				racemosa	Mc-P	e			
Compositae									
Vernonia	Cd	500	8	javanica	I, Ms			i	
Datiscaceae									
Tetrameles	Ms, Ph	1	1	nudiflora	I, NM, J, Ti				d
Dilleniaceae									
Dillenia	As, Au	10	6	aurea	I, Si, NM, J, Ph				d
,,				grandifolia	M				d
,,				indica	I, Si, M			i	
,,				ovata	WMs, IC, T			i	
,,				reticulata	M				d
Wormia	As, Au, Mg	20	4	albiflos	M, NB	e			
,,				excelsa	M, S, B			i	
,,				pulchella	M, S, B			i	
,,				suffruticosa	WMs	e			
Dipterocarpaceae									
Anisoptera	Bu-NG	17	7	megistocarpa	SM, S				d
Dipterocarpus	I-Ce	69	34	grandiflorus	Ad, Si, Ph				d
,,				Kunstleri	S, NM				d
,,				Lowii	M, S, B				d

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Dipterocarpaceae—*contd.*					
Dryobalanops	B, M, S	6	2	aromatica	B, M, S	e			
Hopea	I-NG	56	9	mengarawan	S, SM			i	
Pentacme	Bu-Ph	6	1	siamensis	Bu, Si, IC, NM				d
Shorea	I-Mo, Ph	95	58	Curtisii	Si, M			i	
,,				Hemsleyana	NM			i	
,,				leprosula	Si, M, S, NB				d
,,				(robusta)	I, Bu			i	
,,				sumatrana	A, M			i	
				Ebenaceae					
Diospyros	I-Bu-J, Au	300	70	cordifolia	I, Si, Ms, Au				d
,,				(ebenum)	I, Cy			i	
,,				lanceifolia	WMs			i	
,,				(mollis)	S			i	
,,				oblonga	M			i	
				Elaeocarpaceae					
Elaeocarpus	I, Ms, Au	100	30	ferrugineus	M, B			i	
,,				littoralis	Bu, Si, WMs			i	
,,				Mastersii	WMs			i	
,,				obtusus	Bu, M, S, B			i	
,,				petiolatus	IC, WMs			i	
,,				polystachyus	M, B			i	
,,				sphaericus	I, WMs	e			
,,				stipularis	IC, WMs	e			
				Erythroxylaceae					
Ixonanthes	SEA-MG	11	2	icosandra	M, S			i	
,,				reticulata	M, S, B				d
				Euphorbiaceae					
Acalypha	Tr, SAf	400	3	siamensis	Si, NEM			i	
Agrostistachys	I, Ms, Ph	11	3	sessilifolia	M			i	
(Aleurites)	As, P	5		(moluccana)	Mol	e			
Antidesma	Af, As, Au	140	21	(bunius)	I-Au			i	
,,				(diandrum)	I-Bu			i	
Aporosa	As-NG	60	20	Benthamiana	M-S			i	
,,				bracteosa	M, S, B			i	
,,				nigricans	M			i	
Baccaurea	As, Au	60	22	Kunstleri	M			i	
,,				latifolia	M			i	
,,				macrophylla	M	e			
,,				malayana	M			i	
,,				parviflora	M, S			i	
,,				pyriformis	M			i	
(Bischofia)	I, Ms, Po	2	1	(javanica)	I, Ms, Po				d
Bridelia	ETr	50	8	retusa	I, Si, M				d
,,				tomentosa	I, Ms	e			
Claoxylon	Mg, As, P	57	4	indicum	I, Ms				d
Cleistanthus	Af, I, Ms	110	30	heterophyllus	M			i	
Croton	Cd	500	10	(eleuteria)	Am	e			
,,				(laevifolium)	IO			i	
Elateriospermum	WMs	1	1	tapos	M, S, J				d
Emblica	As, Am	11	1	officinalis	SEA			i	
Euphorbia	Cd	750	10	neriifolia	I, Ms	e			
Excoecaria	ETr	26	3	agalloca	Af-Au				d
Glochidion	As-Au	130	24	laevigatum	M	e			
,,				microbotrys	M	e			
,,				sericeum	M, B, J	e			
,,				singaporense	SM	e			
,,				superbum	SM-Ph	e			

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Euphorbiaceae—*contd.*					
(Hevea)	Amazon	12		(brasilliensis)	Ms				d
(Hura)	Am, WI	2		(crepitans)	SAm			i	
(Jatropha)	Am, Af	150		(multifida)	Am			i	
Macaranga	ETr	200	24	javanica	Si, IC, M, S, J	e			
,,				triloba	WMs	e			
Mallotus	As, Af	100	25	sp.	SM				d
,,				paniculatus	Ch, Si, Au	e			
Microdesmis	As, Af	2	1	(casearifolia)	T, Ch, B	e			
Pimelaeodendron	Ms	4	1	Griffithii	M			i	
Ptycopyxis	Ms	1	1	costata	Ms				
Sapium	Am, As	100	3	discolor	Ch				d
,,				indicum	I, Ms	e			
,,				sebiferum	Ch		m		
				Fagaceae					
Castanopsis	CdAs	40	15	Andersonii	M			i	
,,				inermis	SM			i	
Quercus	Eu, As, NG, Am	400	40	(bambusaefolia)	Ch			i	
,,				conocarpa	WMs			i	
,,				craterophora	M			i	
,,				hysterix	WMs			i	
,,				lucida	WMs			i	
				Flacourtiaceae					
Flacourtia	I, Ms	10	3	indica	I-Mc (not Sm)				d
,,				jangomas	ETr				d
,,				rukam	I, Ms			i	
Homalium	Tr	50	8	grandiflorum	Si, M				d
Hydnocarpus	I-Ms-Ph	30	7	(anthelmintica)	Si, IC			i	
,,				Kurzii	Ass, Bu, T	e			
Pangium	WMs	2	1	edule	Ms				d
				Goodeniaceae					
Scaevola	Au, ETr	2	1	frutescens	I-Po	e			
				Guttiferae					
Calophyllum	Tr	50	25	inophyllum	I-WP			i	
Cratoxylon	As, Ce, Ph	12	5–6	arborescens	WM			i	
,,				formosum	IC, Ms, Ph				d
,,				ligustrinum	I, WM, Ph				d
,,				Maingayi	T, IC, Si, M, S				d
Garcinia	ETr	100	40	atroviridis	Bu, M			i	
,,				(dulcis)	J, B, Ph		m		
,,				(ferruginea)	IC			i	
,,				Forbesii	S, M			i	
,,				Hombroniana	Nic, M			i	
,,				(Livingstonii)	TrAf			i	
,,				mangostana	M			i	
,,				xanthochymus	SEA, Ms			i	
Kayea	I, Ms	12	11	ferruginea	Ad, M			i	
Mesua	I, J	2–3	2	ferrea	Hm-M			i	
(Rheedia)	Am, Mg	17		madruno	CAm	e			

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
Hamamelidaceae									
Altingia	I, Ms, Ch	2	1	excelsa	I, M, J				d
Bucklandia	Hm, Bu, Ms	1	1	populnea	M	e			
Rhodoleia	M, Ch	3	2	ovalifolia	M			i	
,,				Teysmannia	M, S			i	
Juglandaceae									
Engelhardtia	I-Ch, M	10	4	nudiflora	M				d
,,				Wallichiana	M			i	
Lauraceae									
Actinodaphne	EAs, Ms	50	15	bancana	M		m		
,,				malaccensis	SM		m		
Beilschmiedia	Tr	20	15	malaccensis	SM				d
Cinnamomum	As, Au, WP	150	17	(camphora)	Ch, F, Jp		m		
,,				iners	I, WMs		m		
,,				(zeylanicum)	I, Cy		m		
Cryptocarya	Cd	50	17	Griffithii	M, B			i	
Lindera	As, NAm	60	14	lucida	SM, WMs	e			
Litsea	As, Au	200	56	gracilis	M			i	
,,				megacarpa	M			i	
,,				singaporensis	M			i	
Phoebe	As, Am	40	6	grandis	WMs			i	
,,				macrophylla	M			i	
,,				opaca	M, J, S, B			i	
Lecythidaceae									
Barringtonia	Af, As, Au	30	15	asiatica	ETr			i	
,,				(acutangula)	I, Si, IC			i	
,,				racemosa	I, Ms, Po			i	
(Bertholetia)	Br	1		(excelsa)	Br				d
(Couroupita)	Am	4		(guianensis)	Guiana				d
(Lecythis)	Am	45		(ollaria)	TrAm	e			
(Napoleona)	WAf	5		(imperialis)	TrAf			i	
Leguminosae									
(Acacia)	Au, Af	450		(auriculaeformis)	NAu		m		
,,				(catechu)	I, Bu, Si		m		
,,				(confusa)	Ph, F			i	
,,				(glomerosa)	SAm		m		
,,				(interjecta)	WI	e			
Adenanthera	ETr	3	2	bicolor	Cy, M				d
,,				pavonina	I, Ch, Ms, Mo				d
Albizzia	ETr etc	100	4	falcata	EMs	e			
,,				(odoratissima)	Hm, Bu, Cy, Si				d
(Amherstia)	Bu	1		(nobilis)	Bu		m		
(Andira)	Am, Af	25		(inermis)	SAm, WI, WAf			i	
(Baphia)	Af, Mg	30		(nitida)	TrAf			i	
(Brownea)	SAm, WI	15		(ariza)	New Granada		m		
,,				(capitella)	Ven		m		
,,				(coccinea)	Jam		m		
,,				(grandiceps)	Ven		m		
,,				(macrophylla)			m		
(Butea)	SEA, Ch, J	3		(frondosa)	I, Bu, Ch, J				d

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Leguminosae—*contd.*					
Caesalpinia	Tr	100	9	(coriaria)	Am	e			
,,				(ferrea)	Br				d
,,				sappan	I, Ms			i	
Cassia	Tr	400	17	(excelsa)	Br			i	
,,				(fistula)	I, Cy				d
,,				(javanica)	J, S, Ph				d
,,				(leptophylla)	Br				d
,,				(multijuga)	TrAm	e			
,,				nodosa	Bu, Ch, WMs				d
,,				siamea	I, Ms	e			
,,				(splendens)	Am	e			
Cynometra	Tr	20	3	inaequifolia	Si, WMs, Ph			i	
,,				ramiflora	I, Cy, Ms			i	
Dalbergia	As, Au, Po	120	15	(Oliveri)	Bu, Si				d
(Delonix)	Af, Mc	3		(regia)	Mg				d
Dialium	SEA	15	8	Wallichii	M			i	
(Enterolobium)	Am	6		(saman)	SAm	e			
Erythrina	Tr	30	5	fusca	Mc, I, Ms, P				d
,,				indica	I-P				d
,,				lithosperma	Bu, M			i	
,,				subumbrans	Bu, WMs, Ph			i	
(Gliricidia)	Am	4		(sepium)	CAm				d
(Haematoxylon)	Am, WI	1		(campechianum)	Am			i	
(Hymenaea)	Am	8		(courbaril)	WI				d
Inocarpus	Am, Ms, P	1	1	edulis	Ms-P			i	
Intsia	ETr	12	2	Bakeri	Si, WMs, Ce				d
,,				bijuga	Mc-Po				d
Koompassia	IC, Ms	4	2	excelsa	M, S, B				d
,,				malaccensis	M, S				d
(Leucaena)	Am, P	9		(glauca)	SAm	e			
(Lonchocarpus)	Am, Af, Au	120		(cyanensis)	WAf			i	
Millettia	Af, I, Ms, Au	150	15	atropurpurea	Bu, Si, WMs			i	
,,				(Manni)	TrAf			i	
(Mimosa)	Am, As, Af	300		(sepiaria)	SAm	e			
(Myroxylon)	Am	8		(toluiferum)	Am				d
Parkia	Tr	10	3	javanica	Ms				d
,,				speciosa	I-J			i	
Peltophorum	Tr	7	3	dasyrachis	Si, S, M				d
,,				pterocarpum	IC-M-Au				d
(Pentaclethra)	Am, Af	3		filamentosa	Am			i	
,,				(macrophylla)	Af			i	
(Phyllocarpus)	Br	1		(septentrionalis)	Br	e			
(Piptadenia)	TrAm	45		(colubrina)	Br			i	
Pithecellobium	TrAs, TrAm	60	10	ellipticum	WMs			i	
,,				jiringa	WMs			i	
,,				microcarpum	S, M, B			i	
Pongamia	I-Fiji	few	1	pinnata	SEA-P				d
(Prosopis)	Cd	25		(juliflora)	Am	e			
Pterocarpus	Tr	15	1	indicus	Ms				d
Saraca	I-Ms	20	7	bijuga	Si, M			i	
,,				declinata	Si, M, S, J			i	
,,				(indica)	I			i	
,,				thaipingensis	M			i	
(Sesbania)	Tr	40	2	(grandiflora)	EAs	e			
Sindora	I-Ms, Af	9	5	coriacea	M				d
,,				Wallichii	M				d
Sophora	Cd	25	1	tomentosa	I-P			i	
Tamarindus	Af, As	1	1	indica	TrAs				d
(Tetrapleura)	WAf	3		(Thonningii)	TrAf			i	
(Trachylobium)	Af, As	3		(verrucosum)	EAf, Mc			i	

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Loganiaceae					
Fagraea	TrAs, WP	60	20	auriculata	M, J, IC, Ph			i	
,,				fragrans	T, Si, Ms	e			
,,				gigantea	S, SM	e			
,,				Ridleyi	SM			i	
				Lythraceae					
Duabanga	Hm-Ph	2	1	sonneratioides	I-NM	e			
Lagerstroemia	CdAs, Mg, NG, Au	20	3	floribunda	Bu, Si, M				d
,,				flos-reginae	I-Au, NM				d
,,				ovalifolia	WMs				d
Sonneratia	As-P	4–5	3	acida	I-P	e			
,,				alba	I-P	e			
				Magnoliaceae					
(Magnolia)	As, NAm	21		(fusca)	Ch	e			
Michelia	I-Ms	12	5	(alba)	J	e			
,,				champaca	I, M	e			
				Malvaceae					
Hibiscus	Tr	150	12	macrophyllus	IC, Si, WMs	e			
,,				(rosa-sinensis)	Ch?	e			
,,				(schizopetalus)	EAf	e			
,,				tiliaceus	Tr	e			
Thespesia	Af, As Au	6	1	populnea	ETr	e			
				Melastomaceae					
Memecylon	ETr	150	35	heteropleurum	M, S, B			i	
Pternandra	Ms	18	5	capitellata	T-M			i	
,,				coerulescens var. Jackiana	WMs-Mol			i	
,,				echinata	M, B	e			
				Meliaceae					
Aglaia	I, Ms, Au	90	40	trichostemon	M, B	e			
Carapa	Tr	6	3	(guianensis)	SAm		m		
Cedrela	As, Am	16	3	(glaziovii)	Am				d
Chisocheton	I, Ms	30	11	spicatus	M			i	
(Chloroxylon)	I, Cy	1		(swietenia)	I, Cy				d
Melia	ETr	12	4	(azedarach)	Hm			i	
(Swietenia)	Am	5		(macrophylla)	Hond			i	
,,				(mahogani)	WI			i	
				Moraceae					
Antiaris	Af, I, Ms	3–4	1	toxicaria	I, Ch, Ms				d
Artocarpus	As-P	50	20	bracteatus	NM				d
,,				(communis)	P	e			
,,				dadah	WMs				d
,,				Gomezianus	WMs			i	
,,				rigida	WMs			i	
(Castilloa)	Am, Cuba	3		(panamensis)	Mx, Per	e			
(Cecropia)	SAm	30–40		(peltata)	SAm	e			

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Moraceae—*contd.*					
Ficus	Cd	600	100	alba	WMs	e			
,,				(calophyllus)	J			i	
,,				caulocarpa	I-Ms				d
,,				elastica	Hm-J	e			
,,				glomerata	As, WMs				d
,,				indica	I, Ms			i	
,,				(irregularis)	Ce			i	
,,				(Kurzii)	J			i	
,,				lepicarpa	WMs			i	
,,				religiosa	Hm I				d
,,				superba	WMs				d
,,				variegata	I, Ch, WMs, Ph				d
Streblus	I, M, SCh, Ph	2	1	asper		e			
				Myricaceae					
Myrica	Cd	40	1	Farquhariana	M			i	
				Myristicaceae					
Horsfieldia	As-NG	55	19	globularia	M, J, Ce	e			
,,				(grandis)	Cy			i	
,,				(sylvestris)	Cy	e			
				Myrsinaceae					
Aegiceras	As, Au	2	1	corniculatum	I-NG	e			
				Myrtaceae					
(Eucalyptus)	Au, EMs	200		(corymbosa)	Au			i	
,,				(longifolia)	Au	e			
,,				(Naudiniana)	Au	e			
,,				(robustus)	Au	e			
Eugenia	Tr	1,000	150	(aromatica)	Mo		m		
,,				densiflora	WMs			i	
,,				javanica	Ad, WMs			i	
,,				(liliiformis)				i	
,,				longiflora	WMs			i	
,,				malaccensis	Ms			i	
,,				myrtifolia	I, M			i	
,,				polyantha	Bu, WMs			i	
,,				Ridleyi	M			i	
,,				spicata	I-J			i	
Melaleuca	Au, Ms, M	130	1	leucodendron	T, WMs, Mol			i	
(Psidium)	Am	120		(guajava)	TrAm			i	
Rhodamnia	Tr	60	2	trinervia	T-Au			i	
				Nyctaginaceae					
Pisonia		60	2	(alba)	Ms (not M)			i	
,,				excelsa	Ms				d
				Ochnaceae					
Ouratea	SAm	80	4	corymbosa	M			i	
,,				crocea	M			i	

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
Olacaceae									
Gonocaryum	Bu, M	4	2	longe-racemosum	M	e			
Ochnostachys	B, M	1–2	1–2	amentacea	B, M			i	
Scorodocarpus	M, B	1	1	borneensis	B			i	
Oxalidaseae									
Averrhoa	Ms	2	2	bilimbi	Ms	e			
,,				carambola	J, EMs	e			
Connaropsis	M, B	8	8	Griffithii	M			i	
,,				macrophylla	M			i	
Pittosporaceae									
Pittosporum	ECd	60	3	(tobira)	Ch			i	
Polyglaceae									
Xanthophyllum	Ms, I, Au	30	21	Curtisii	M			i	
Polygonaceae									
(Triplaris)	SAm	10		(americana)	SAm	e			
,,				(surinamensis)	SAm	e			
Proteaceae									
Buckinghamia	Q	1		(celsissima)	Au			i	
(Grevillea)	Au	170		(robusta)	Au			i	
(Stenocarpus)	EAu, NC	15		(sinuatus)	Au			i	
Rhamnaceae									
Zizyphus	Cd	100	10	calophylla	M, B, S			i	
,,				(Jujuba)	I-Ch			i	
,,				(mauritiana)	IO		m		
Rhizophoraceae									
Anisophyllea	TrAs, Af	10	7	disticha	WMs	e			
,,				Griffithii	M			i	
Bruguiera	As-EAf	5	4	gymnorhiza	ETr	e			
Ceriops	ETr	1	1	Candolleana	ETr	e			
Gymnotroches	Si, Ms	2	1	axillaris	M	e			
Kandelia	I, Ms	1	1	Rheedii	Ms	e			
Rhizophora	Cd	3	2	conjugata	ECd	e			
,,				mucronata	ECd	e			
Rosaceae									
Parinarium	Tr	50	12	corymbosum	Ms			i	
Pygeum	WAf	30	15	parviflorum	WMs			i	
,,				polystachyum	NM				d
Pyrus	NTemp-TrMt	70	1	granulosum	I-Ms				d
Rubiaceae									
Adina	ECd	10	2–3	rubescens	M				d
Anthocephalus	I, Ms	2	1	cadamba	I-NM				d
Canthium	ETr	100	10	dicoccum	SEA-Ms	e			
,,				glabrum	Si, M	e			

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Rubiaceae—*contd.*					
Gardenia	ETr-Temp	70	10	carinata	M	e			
,,				(coronaria)	Bu	e			
Ixora	ETr	120	20	congesta	T, M	e			
,,				multibraceteata	SSi, M	e			
Jackia	M, S, B	1	1	ornata	M	e			
Morinda	Tr	50	7	citrifolia	I, Ms, P	e			
,,				elliptica	M	e			
Randia	Tr	100	25	anisophylla	S, M, B	e			
,,				macrophylla	S, M			i	
Scyphiphora	As, Au	1	1	hydrophyllacea	As, Au	e			
Timonius	As, Po	30	10	Wallichianus	M	e			
Urophyllum	As, Af	40	13	hirsutum	M			i	
,,				streptopodium	M	e			
				Rutaceae					
(Aegle)	I	1		(marmelos)	I	e			
Atalantia	Hm, Au	10	6	spinosa	I, Bu, Si, M			i	
Feronia	I, Si	1	1	limonia	I, Si				d
Glycosmis	SEA, Ms	20	8	chlorosperma	WMs			i	
				Salicaceae					
(Salix)	Cosm	160		(tetrasperma)	I-Ch				d
				Sapindaceae					
Erioglossum	As-Af	4	1	rubiginosum	M			i	
(Filicium)	As-Af	3		(decipiens)	I, Cy	e			
Guioa	I, Ms, Au	60	4	pubescens	WMs, Ph			i	
Lepisanthes	As	20	5	cuneata	M			i	
(Litchi)	Ch	1		(chinensis)	Ch			i	
Nephelium	As, Au	70	16	lappaceum	Ms			i	
,,				ophioides	M			i	
Paranephelium	I-Ms	8	3	macrophyllum	Si, NM			i	
Pometia	I, Ms, Au	7	4	pinnata	I, Ms, Po			i	
Trigonachras	Ph, M	9	1	acuta	SM				d
Xerospermum	I-Ms	20	6	muricatum	M			i	
				Sapotaceae					
Achras)	Mx, CAm	1		(zapota)		e			
Lucuma	Am, As	50	8	Maingayi	M, S, B				d
Madhuca	I-Ms	40	21	Kingiana	M			i	
Mimusops)	ETr	20	2	(elengi)	I, Bu, Cy			i	
Palaquium	I, Ms, Po	100	14	Clarkianum	M				d
,,				gutta	S, M, B	e			
,,				Maingayi	M				d
,,				obovatum	T, M, S				d
Payena	Ms	12	12	dasyphylla var. glabra	M, J, S	e			
(Pouteria)	Am	30		(suavis)	Uruguay			i	
				Simarubaceae					
Eurycoma	IC, Ph, B	2	2	longifolia	IC-M, S, B			i	
Irvingia	Af-Ms	4	1	malayana	IC-M, S, B				d
				Solanaceae					
Solanum	Cd	1,225	16	(Wrighti)	Bolivia	e			

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
				Sterculiaceae					
(Cola)	Af	50		(acuminata)	TrAf	e			
Commersonia	Au, P, Ms, Ch	8	1	Bartramia	Ch, Ms, P	e			
(Dombeya)	Af	100		spectabilis	TrAf	e			
Firmiana	I-Ms	2	1	fulgens	M				d
Heritiera	As, Af, Au	7	2	elata	M				d
,,				littoralis	I-P			i	
,,				(macrophylla)	Bu				d
Kleinhovia	Mc-Po	1	1	hospita	M				d
Pterocymbium	Bu, WMA Ph	2	2	javanicum	Bu-Ph				d
,,				tubulatum	M				d
(Rheevesia)	Hm-Ch	3		(thyrsoidea)	Ch	e			
Scaphium	Bu, IC, M, B	4	3	affine	M				d
,,				linearicarpum	M				d
Sterculia	Tr	200	20	(carthaginensis)	Am				d
,,				ferruginea	Ph				d
,,				foetida	Af-Au				d
,,				macrophylla	WMs				d
,,				parviflora	I M				d
,,				rubiginosa	I, IC, WMs				d
Tarrietia	I, Ms, Au	10	6	javanica	WMs			i	
				Symplocaceae					
Symplocos	Cd	300	30	fasciculata	M, S, B, J	e			
,,				rubiginosa	WMs			i	
				Theaceae					
Adinandra	SEA	20	10	acuminata	Ms			i	
,,				angulata	NM (highland)			i	
,,				dumosa	M, S, J, B	e			
,,				Hulletti	SM			i	
,,				integerrima	M, IC			i	
,,				macrantha	M (mountain)			i	
,,				maculosa	M (mountain)			i	
,,				parvifolia	M (mountain)			i	
,,				villosa	M (mountain)			i	
Archytaea	TrAm, Ms	4	2	Vahli	Si, Ms	e			
Gordonia	CdAs, Am	20	10	penangensis	M			i	
,,				singaporeana	M			i	
Pyrenaria	I-M	7	2	acuminata	M			i	
Ternstroemia	As, Am	300	6	bancana	M			i	
(Thea)	SEA, Ch, Jp	40		(cochin-chinensis)	IC			i	
				Thymeliaceae					
(Phaleria)	I-Ms	12		(Blumei)	S, J, B, Ce, Mo			i	

Genera	Distribution	No. of species	Do. of Malaya	Species	Localities	e	m	i	d
Ulmaceae									
Gironniera	SEA	12	4	nervosa	WMs (not Java)				d
,,				subaequalis	SEA	e			
Trema	Tr	30	3	angustifolia	WMs	e			
,,				orientalis	Hm-Po	e			
,,				variegata	SEA-Ms	e			
Verbenaceae									
Avicennia	Tr	4	4	alba	I-Ms	e			
,,				intermedia	M	e			
,,				lanata	M	e			
,,				officinalis	I-Po	e			
Callicarpa	Tr	50	7	(Rheevesii)	SCH	e			
(Citharexylum)	Am	20		(quadrangulare)	Am			i	
Gmelina	As, Au	12	1	(arborea)	I			i	
Premna	ECd	50	13	tomentosa	I-WMs, Ph, Tim			i	
(Tectona)	I, Bu, Si, Ph	3		(grandis)	Bu, Si, EJ, Ph		m		
,,				(Hamiltoniana)	I			i	
Vitex	Cd	140	16	(capitata)	TrAm		m		
,,				coriacea	NM			i	
,,				pubescens	TrAs		m		
Violaceae									
Alsodeia	Tr	50	19	Maingayi	SM			i	
Vitaceae									
Leea	As, Af, Au	70	12	aequata	WMs	e			
,,				angulata	WMs	e			
,,				indica	I-P	e			
,,				rubra	IC-J, NM	e			

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